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INFLUENCE OF LIGHT AND TEMPERATURE ON SUGARCANE AND ERIANTHUS[1]

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INTRODUCTION

In a previous publication (*2*, *p. 3*),[2] dealing with the photothermal requirements of sugarcane, evidence was submitted that "at given temperatures there are definite light requirements, the light needs being greater at the higher temperatures and less at lower temperatures." For example, at 59° F., when three 40-watt fluorescent daylight tubes and two 100-watt Mazda bulbs were used as the source of light, the plants showed slight growth and continued in fairly normal health for 8 weeks; whereas, with the same light source at 78°, there was little growth and marked impairment of health, death resulting in many cases. At 59° the anabolic and catabolic processes of the plants were in approximate balance, whereas at 78° the catabolic processes exceeded the anabolic, especially during the later weeks of the experiment. As the light intensity at 78° was increased, there was a marked improvement in the health and growth of the plants. The existence of a fundamental relation between the factors of light and temperature in their effects upon the development of plants was revealed by the writers in these earlier experiments and led to the further studies reported in the present paper. Bolas (*1*) found a similar relation between temperature and light intensity and assimilation rate (measured by change in dry weight) in tomato plants during a period of 7 hours.

The investigations reported in this paper and in a previous one (*2*) included (1) studies on the rate of growth of a group of wild and garden varieties of sugarcane, indigenous to different latitudes, that were assembled and studied individually at a series of stations at various locations extending from the Equator to latitude 40° N., and (2) rate-of-growth studies of some of these same varieties as well as additional ones under controlled conditions of temperature and light. From November 19, 1940, to July 11, 1941, five experiments were conducted at the United States Department of Agriculture Cold Storage Laboratory, Arlington Experiment Farm, Arlington, Va.

MATERIALS AND METHODS

The plants used in the present studies included 3 varieties of erianthus and 21 varieties of sugarcane, 8 of which had been used in the rate-of-growth studies (table 1). The experimental environmental conditions included additional temperatures and a wider range of

[1] Received for publication March 22, 1944.

[2] Italic numbers in parentheses refer to Literature Cited, p. 18.

light intensities than was previously employed. The plant materials for the most part were selected with consideration for the significance of latitude in growth and light-temperature relations, and selection was limited to forms known with reasonable certainty to have originated at particular latitudes.

TABLE 1.—*Statistics on varieties of sugarcane and erianthus studied*

Species and variety [1]	Wild or garden	Importation No.	Place of origin	Latitude where indigenous
Erianthus arundinaceus (Retz.) Jesw.:				
28 N.G. 7	Wild	631	Territory of Papua, New Guinea	8° S.
Erianthus maximus Brongn.:				
N.C. 132 [2]	do	921	New Caledonia, French Oceania	21° S.
Raistea [2]	do	923	Society Islands, French Oceania	17° S.
Saccharum barberi Jesw.: Hatooni	Garden	213	British India	25° N.
Saccharum officinarum L.:				
Caña Criolla [2]	do	615	do	11° N.
Louisiana Purple	do	5	Java, Dutch East Indies	6° S.
N.C. 25 [2]	do	888	New Caledonia, French Oceania	21° S.
N.C. 117	do	909	do	21° S.
"*Saccharum robustum*": N.H. 1	Wild	933	New Hebrides, South Pacific	17° S.
Saccharum sinense Roxb.: Cayana [2]	Garden	126	British India	31° N.
Saccharum spontaneum L.:				
Burma [2]	Wild	848	do	20° N.
Djatiroto	do	569	Java, Dutch East Indies	8° S.
Gehra Bon	do	618	British India	25° N.
Pasoeroean	do	555	Java, Dutch East Indies	8° S.
Rellagadi	do	617	British India	19° N.
Tabongo [2]	do	578	North Celebes, Dutch East Indies	0°.
U.S. 4515 [2]	do		Turkmenistan, Union of Soviet Socialist Republics.	40° N.
Saccharum hybrids: [3]				
Co. 281	Garden	176	Coimbatore, British India	11° N.
C.P. 1165	(4)		Canal Point, Fla	27° N.
C.P. 29/291	(4)		do	27° N.
C.P. 31/294	(4)		do	27° N.
C.P. 31/511	Garden		do	27° N.
C.P. 34/79	(4)		do	27° N.
P.O.J. 2725	Garden		Java, Dutch East Indies	8° S.

[1] Varieties of sugarcane are often designated by letters or other abbreviations that usually indicate place or institution of origin. The meanings of designations used in this paper are as follows: Co., Coimbatore (India); C.P., Canal Point (Fla.); N.C., New Caledonia; N.G., New Guinea; N.H., New Hebrides; P.O.J., Proefstation Oost Java; and U.S., United States.

[2] Used in rate-of-growth studies.

[3] The hybrids were derived from both wild and garden stock of sugarcane.

[4] Bred at Canal Point, Fla., but not released for commercial cultivation.

Nine insulated rooms (eight of them approximately 7 by 14 feet by 11 feet high and one approximately 8 by 9 feet by 8 feet high) provided space for the controlled conditions (one condition of light intensity to each room) during the first three experiments; seven of the larger rooms provided space during the fourth experiment. The control rooms were cooled by brine coils, and the temperature was maintained within 4° F. (mostly within less than 2°) by the use of thermostatically controlled electric heaters.

Air exchange was provided in each room by forcing air through a 2-inch duct that led to the rear of the room. A similar duct through the front wall permitted escape of the air. The air was exchanged about once every hour. The relative humidity in the rooms varied from about 60 to 80 percent, the percentage tending to increase with lowering of the temperature.

The light source in each room was a combination of Mazda lamps and daylight fluorescent tubes. In eight of the nine rooms used the lights were mounted on a frame attached to pulleys for raising or lowering the light source to the desired height (1 foot) above the tops

of the plants. The lights in each room were arranged so as to distribute the light at as uniform intensity as possible over an area of 24 square feet (4 by 6 feet), the space occupied by the plants. In the ninth room the lights were stationary at about 4 to 5 feet above the tops of the plants. This room was the source of the lowest light intensity employed and was used only in connection with temperatures of 60° and 65° F. In none of the rooms was the light intensity uniform over the entire area occupied by the plants.

This variation in intensity was influenced particularly by the position of the Mazda lamps. The approximate intensities corresponding to the number and combinations of Mazda and fluorescent lights used in experiments 1 to 4 are shown in table 2. It should be kept in mind that the light intensities employed in all these experiments were relatively low as compared with normal outside light. In all experiments the daily light and dark periods were 13 and 11 hours, respectively.

TABLE 2.—*Source and approximate intensities of light used in experiments 1 to 4*

[Some of the intensities were duplicated at the different temperatures employed]

Light source					Approximate intensity 1 foot from source [1]
Fluorescent tubes			Mazda bulbs		
Total	Length	Power	Total	Power	
Number	*Inches*	*Watts*	*Number*	*Watts*	*Foot-candles*
1	24	20	1	50	20
2	48	40	1	100	50
4	48	40	2	100	100
9	48	40	4	100	220
18	48	40	8	100	340
35	48	40	16	100	500

[1] The source for the lowest light intensity used (20 foot-candles) was about 4 to 5 feet above the plants.

The source of light in experiment 5 was water-cooled, 1,000-watt Mazda lamps suspended, by a pulley arrangement for altering the height of the light, in chambers (18 inches square and 12 feet high) that were provided with air exchange. These lamps furnished an intensity of about 1,750 foot-candles at the top of the plants. The 200-foot-candle intensity was obtained by covering the lights with paper or muslin. The light intensities were measured 1 foot below the light source. In experiments 1 to 4 there was one light intensity (100 foot-candles) common to all temperatures. In the first three experiments there was one additional intensity (50 foot-candles) common to the two lower temperatures (60° and 70° F.) and one additional intensity (220 foot-candles) common to the two higher temperatures (70° and 78° in experiment 1, and 70° and 86° in experiments 2 and 3).

In addition to growing the different varieties of sugarcane and erianthus under the foregoing conditions of light and temperature, in two of the experiments control plants were grown in the greenhouse.

The plants were grown from stem cuttings in 4-inch pots in a greenhouse. About 10 to 14 days before the plants were exposed to the various conditions of light and temperature they were transferred to 6-inch pots. The cuttings were planted and the plants exposed to experimental conditions of temperature and light on the following

dates: Experiment 1, August 20 and November 19, 1940; experiments 2 and 5, October 8, 1940, and January 10, 1941; experiment 3, January 29 and March 25, 1941; and experiment 4, April 10 and June 13, 1941. The age of the plants at the beginning of the experiments was as follows: Experiment 1, 91 days; experiments 2 and 5, 94 days; experiment 3, 55 days; and experiment 4, 64 days.

Plants of a given variety in a given experiment were fairly uniform in size, but the sizes differed considerably between varieties, especially in the experiments in which the older plants were used. When dealing with a collection of varieties such as those used in these experiments, it is impossible, although highly desirable, to obtain plants of different

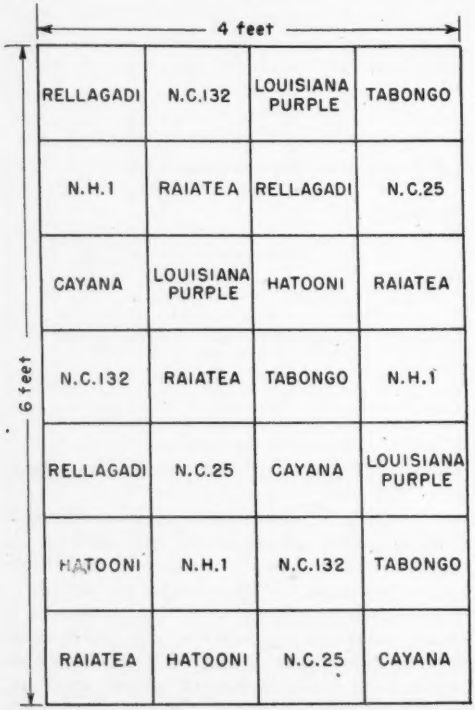

FIGURE 1.—Distribution in each room, beneath the source of light, of individual plants of the different varieties of sugarcane and erianthus used in experiment 3. Similar distributions were made in experiments 1, 2, and 4.

varieties of uniform size. The procedure followed was to grow the plants under uniform conditions and then select within a given variety for uniformity.

In order to compensate somewhat for the variation in light intensity at different points under the batteries of lights, the plants of a given variety were distributed in the same manner in each room (fig. 1).

The number of plants used at each condition of light and temperature in experiments 1 to 4 was 24, 32, 28, and 32, respectively. In most instances 2 plants of each variety were used in experiment 1, and 3 plants of each variety in each of experiments 2, 3, and 4 (see figs. 2 to 5). In each room the plants were arranged in a rectangular area (4 by 6 feet) directly under the lights, with 4 rows one

way and 6, 7, or 8 rows the other, depending upon the number of plants used. The pots containing the plants rested on an open rack, 6 inches above the floor. Daily attention was given to the water requirements of the plants; and, although the soil was not maintained at a constant water content, an effort was made to approximate the same water content in all pots. A record was kept of the amount of water added.

In experiment 5 only one plant of each of two varieties was exposed to each of two light intensities.

Weekly measurements of the height of the plants were taken, and observations were made on the color, health, and death of the leaves and on death of the plants. At the completion of the experiments, dry-weight determinations were made under comparable conditions of drying (floor of attic in the headhouse of a greenhouse).

EXPERIMENTAL DATA

The data here reported deal with species and varieties of two closely related genera, *Saccharum* and *Erianthus* (table 1). Each is vegetatively propagated and is commonly regarded and designated as a variety. In the illustrations and tables dealing with the response of the plants to light and temperature, the varieties are listed alphabetically, regardless of specific and generic connections. Because of the common response of all varieties, the discussion, in the main, will deal with the response of the varieties as a group.

TABLE 3.—*Total average increase in height per plant of mother stalks plus suckers and of mother stalks alone in different varieties of sugarcane and erianthus exposed for 7 weeks to various conditions of light and temperature in 3 experiments* [1]

MOTHER STALKS PLUS SUCKERS

Experiment No. and variety	Average initial height of mother stalk	Increase in height with indicated light intensity (foot-candles) at—									Greenhouse controls
		60° F.			70° F.			78° or 86° F.[2]			
		20	50	100	50	100	220	100	220	340	
Experiment 1:	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*
Burma	117.0	16.0	18.8	36.5	33.8	39.8	89.5	36.5	63.8	131.8	.....
Cayana	39.5	.5	1.3	3.2	1.8	6.2	18.0	4.3	14.7	47.7	.....
Gehra Bon	48.0	2.0	7.3	17.3	5.0	16.3	34.0	15.3	13.5	36.5	.....
Hatooni	36.5	1.0	1.3	4.0	1.8	4.0	9.3	2.8	6.0	25.8	.....
Louisiana Purple	24.0	.....	.3	.3	.3	0	2.0	.5	1.5	7.0	.....
N.C. 132	39.0	.....	6.0	9.5	5.5	9.8	22.3	5.8	30.0	39.0	.....
N.H. 1	63.0	1.3	7.0	16.3	10.3	26.3	42.3	24.0	51.3	63.0	.....
Pasoeroean	74.0	1.8	11.5	22.8	11.3	19.3	36.8	28.0	103.0	104.8	.....
Rellagadi	84.5	23.8	46.8	69.3	24.5	53.3	74.5	20.5	79.8	146.5	.....
Tabongo	76.0	5.8	21.3	18.7	19.8	48.7	80.8	47.7	91.8	136.8	.....
28 N.G. 7	27.5	0	.5	0	.8	1.0	19.0	1.0	10.3	29.0	.....
Total	.....	52.2	122.1	197.9	114.9	224.7	428.5	186.4	465.7	767.9	.....
Experiment 2:											
Burma	37.1	2.5	15.3	14.5	5.8	10.8	23.8	3.0	29.0	61.8	.....
Cayana	24.3	.5	1.2	4.2	2.3	2.7	7.7	8.8	13.7	39.8	.....
Hatooni	22.4	.5	1.5	1.3	.8	1.5	4.7	.8	15.3	12.2	.....
Louisiana Purple	15.4	.3	1.5	0	.3	1.0	.7	.7	3.0	4.8	.....
N.C. 25	14.7	.3	.2	.7	.8	.2	1.7	.3	7.7	6.2	.....
N.C. 132	27.0	1.2	7.5	11.3	10.8	11.0	18.8	11.0	31.0	35.8	.....
N.H. 1	35.9	3.2	5.8	12.0	8.5	17.0	25.2	7.5	42.0	46.5	.....
Pasoeroean	47.9	1.7	7.0	13.8	11.0	20.7	42.5	17.5	72.0	89.2	.....
Raiatea	21.9	1.2	1.5	4.0	4.0	11.7	21.7	3.2	30.8	53.2	.....
Tabongo	53.7	3.2	9.5	15.5	17.8	28.0	43.8	30.3	78.5	109.5	.....
U.S. 4515	39.9	.2	2.3	.7	1.3	.5	5.2	1.0	1.2	3.8	.....
Total	.....	14.8	53.3	78.0	63.4	105.1	195.8	84.1	324.2	462.8	.....

See footnotes at end of table.

TABLE 3.—*Total average increase in height per plant of mother stalks plus suckers and of mother stalks alone in different varieties of sugarcane and erianthus exposed for 7 weeks to various conditions of light and temperature in 3 experiments* [1]—Con.

MOTHER STALKS PLUS SUCKERS—Continued

Experiment No. and variety	Average initial height of mother stalk	Increase in height with indicated light intensity (foot-candles) at—									Greenhouse controls
		60° F.			70° F.			78° or 86° F.[2]			
		20	50	100	50	100	220	100	220	340	
Experiment 3:	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*
Cayana	14.1	0	0.3	0.5	0.3	0.8	6.7	0.7	15.0	24.0	44.3
Hatooni	19.8	.3	.8	1.2	.3	1.3	6.5	.7	8.3	17.5	54.8
Louisiana Purple	12.2	.3	.5	.8	.3	.8	5.7	.5	3.5	11.2	14.5
N.C. 25	10.9	0	.5	.5	.5	1.2	3.3	2.2	5.5	10.3	29.5
N.C. 132	10.2	.8	.8	1.8	1.3	5.2	12.3	4.7	17.5	24.0	33.5
N.H. 1	12.5	.3	1.3	1.0	0	3.7	24.0	.5	12.5	39.3	55.0
Raiatea	13.5	.4	.9	3.5	.6	.9	14.8	.9	17.4	25.4	.....
Rellagadi	10.9	1.0	2.0	6.8	3.3	6.3	30.8	4.0	7.2	32.5	172.2
Tabongo	11.3	1.2	3.1	7.7	2.5	7.3	24.3	4.0	22.8	62.2	99.3
Total	.....	4.3	10.2	23.8	9.1	27.5	128.4	18.2	109.7	246.4	503.1

MOTHER STALKS ALONE

Experiment 1:											
Burma	117.0	14.8	15.3	34.5	30.0	35.3	52.3	28.0	55.0	122.8	.....
Cayana	39.5	.5	.8	3.0	1.8	6.2	13.3	5.3	13.0	40.0	.....
Gehra Bon	48.0	.5	2.8	10.5	2.5	8.0	14.3	6.8	4.5	12.0	.....
Hatooni	36.5	.6	1.0	2.3	1.3	2.0	4.0	2.3	3.8	10.0	.....
Louisiana Purple	24.0	.....	.3	.3	.3	0	2.0	.5	1.5	7.0	.....
N.C. 132	39.0	.....	4.8	9.5	5.5	9.8	22.3	5.8	30.0	39.0	.....
N.H. 1	63.0	1.2	7.0	16.3	10.3	26.0	42.3	24.0	51.3	63.0	.....
Pasoeroean	74.0	1.3	11.0	22.5	11.0	18.3	33.8	26.3	102.0	97.0	.....
Rellagadi	84.5	5.2	8.0	13.3	13.8	22.8	23.0	7.0	47.8	39.8	.....
Tabongo	76.0	3.5	7.0	8.5	11.3	26.0	37.0	23.7	64.5	58.5	.....
28 N.G. 7	27.5	0	.5	0	.8	1.0	19.0	1.0	10.3	29.0	.....
Total	.....	27.6	58.5	120.7	88.6	155.4	263.3	130.7	383.7	518.1	.....
Experiment 2:											
Burma	37.1	1.3	13.0	11.8	5.3	10.9	23.8	3.0	6.0	46.5	.....
Cayana	24.3	.5	1.2	1.8	1.7	1.7	5.8	1.0	4.5	28.2	.....
Hatooni	22.4	.5	1.5	1.3	.8	1.0	4.7	.8	2.7	12.2	.....
Louisiana Purple	15.4	.3	1.5	0	.3	1.0	.7	.7	3.0	4.8	.....
N.C. 25	14.7	.3	.2	.7	.8	.2	1.7	.3	4.0	6.2	.....
N.C. 132	27.0	1.2	7.5	11.3	10.8	11.0	18.8	7.3	28.8	32.3	.....
N.H. 1	35.9	3.2	5.8	12.0	8.5	17.0	22.5	4.8	36.8	46.2	.....
Pasoeroean	47.9	1.7	7.0	13.2	10.5	17.3	38.5	7.3	60.2	69.3	.....
Raiatea	21.9	1.2	1.3	3.7	2.8	7.8	16.3	3.2	29.8	33.3	.....
Tabongo	53.7	1.8	4.7	7.8	8.3	17.7	20.2	12.2	28.2	47.7	.....
U.S. 4515	39.9	.2	.5	0	.2	.3	2.8	.3	1.0	.8	.....
Total	.....	12.2	44.2	63.6	50.0	85.9	155.8	40.9	205.0	327.5	.....
Experiment 3:											
Cayana	14.1	0	.3	.3	.3	.7	6.7	.7	3.5	21.2	17.8
Hatooni	19.8	.3	.5	1.2	.3	1.0	6.5	.8	3.7	17.5	14.5
Louisiana Purple	12.2	.2	.5	.8	.3	.8	5.7	.7	3.5	11.2	14.5
N.C. 25	10.9	0	.5	.5	.5	.7	3.3	2.2	5.7	10.0	11.5
N.C. 132	10.2	.8	.8	1.8	1.3	5.2	12.3	1.7	17.5	23.8	16.8
N.H. 1	12.5	.3	1.3	1.0	0	3.7	24.0	.5	12.5	39.3	51.3
Raiatea	13.5	.1	.6	.8	.3	.9	12.0	.6	17.1	25.4	.....
Rellagadi	10.9	.7	1.0	3.7	1.2	3.0	17.8	1.3	4.0	22.2	33.5
Tabongo	11.3	.3	2.0	5.8	2.2	5.5	15.7	2.3	20.8	50.0	36.0
Total	.....	2.7	7.5	15.9	6.4	21.5	104.0	10.8	88.3	220.6	195.9

[1] The experiments were conducted during the following periods: Experiment 1, Nov. 19, 1940, to Jan. 7, 1941; experiment 2, Jan. 10 to Feb. 28, 1941; and experiment 3, Mar. 25 to May 13, 1941.
[2] The temperature was 78° during experiment 1 and 86° during experiments 2 and 3.

The behavior of the three varieties of *Erianthus* (28 N.G. 7, N.C. 132, and Raiatea) at the various temperatures and light intensities was sufficiently similar to that of certain varieties of *Saccharum* (Gehra Bon, Hatooni, and N.H. 1) to make it impracticable to separate them on a generic basis (table 3). The data do not clearly indicate a distinction between varieties of the different species of *Saccharum*, although the light intensities employed may have been more depressing in their effect on the varieties of *Saccharum officinarum* as a group than on the varieties of the other species of *Saccharum*. Large differences between varieties of *Saccharum*

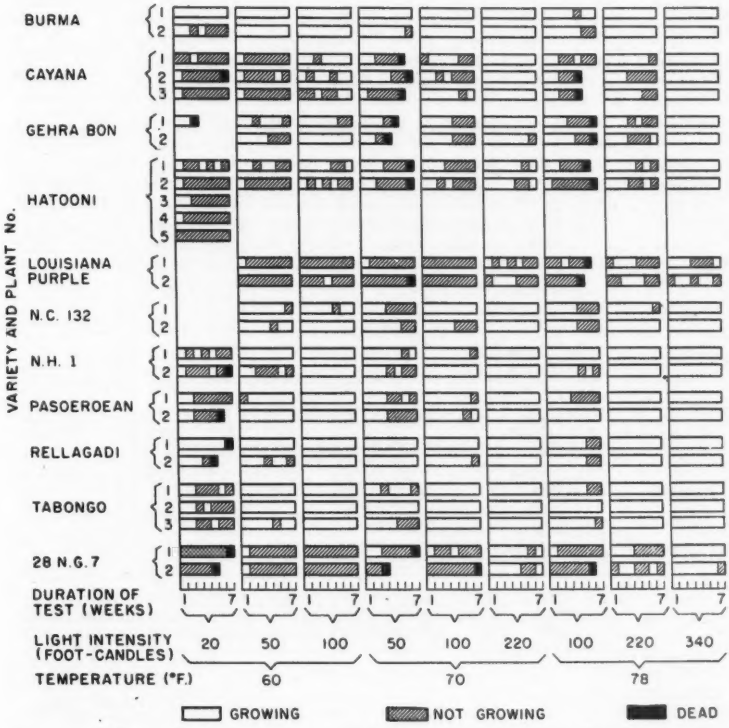

FIGURE 2.—Response of different varieties of sugarcane and erianthus to light intensities at different temperatures in experiment 1. Two plants of U. S. 4515 were used to make up the 24 plants at 20 foot-candles at 60° F., but the data are not represented in the graph.

spontaneum in response to light and temperature were observed. The response of the varieties of the other species of *Saccharum* closely paralleled that of some of the varieties of *Saccharum spontaneum*.

The behavior of plants of all the varieties used in experiments 1 to 3 relative to the presence and absence of growth and the cessation of life at all conditions of light and temperature is shown graphically in figures 2 to 4.

Although temperatures of 60° and 65° F. are near the lower temperature limit for growth of sugarcane, plants grown at these temperatures were, on the whole, more normal than those grown under comparable light intensities at 70° and were in much better health than those grown at the same light intensities at 78° and 86°. The results show clearly that at 78° and 86° and even at 70° a greater light intensity is required for survival, at least during the period covered by these experiments. The contrast in appearance of the plants grown at 65° and those grown at 86° with the same light source (100 foot-candles) in experiment 4 is strikingly illustrated in figure 5. The plants grown

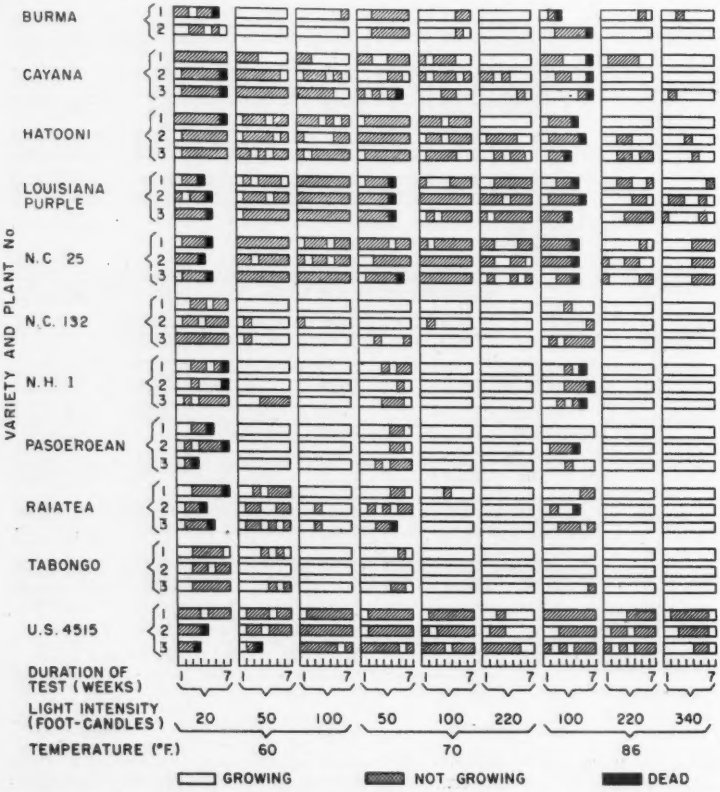

FIGURE 3.—Response of different varieties of sugarcane and erianthus to light intensities at different temperatures in experiment 2.

at 65° showed greater health and less mortality than those grown at 86°. At a light intensity of 100 foot-candles at 60°, growth occurred during more periods (weekly) and more continuously in plants of most varieties in experiments 1 and 2 than at 60° and 65° in experiments 3 and 4 (figs. 2 to 5). At the same intensity at 86°, the plants in experiment 3 were weaker and in many instances death occurred earlier than in plants of the same variety in experiment 2. Associated

with this difference in vital response in the different experiments was a difference in the age of the plants at the beginning of the experiments.

Growth was continuous in most varieties at light intensities of 340 foot-candles at 78° F., 340 and 500 foot-candles at 86°, and 220 foot-candles at 70°.

In addition to the graphically represented distinction between plants exposed to the same light intensity (100 foot-candles) at different temperatures, there was a striking difference in the appearance of the plants. Although growth was not great at 60° and 65° F., the plants, on the whole, exhibited a good green color and appeared nor-

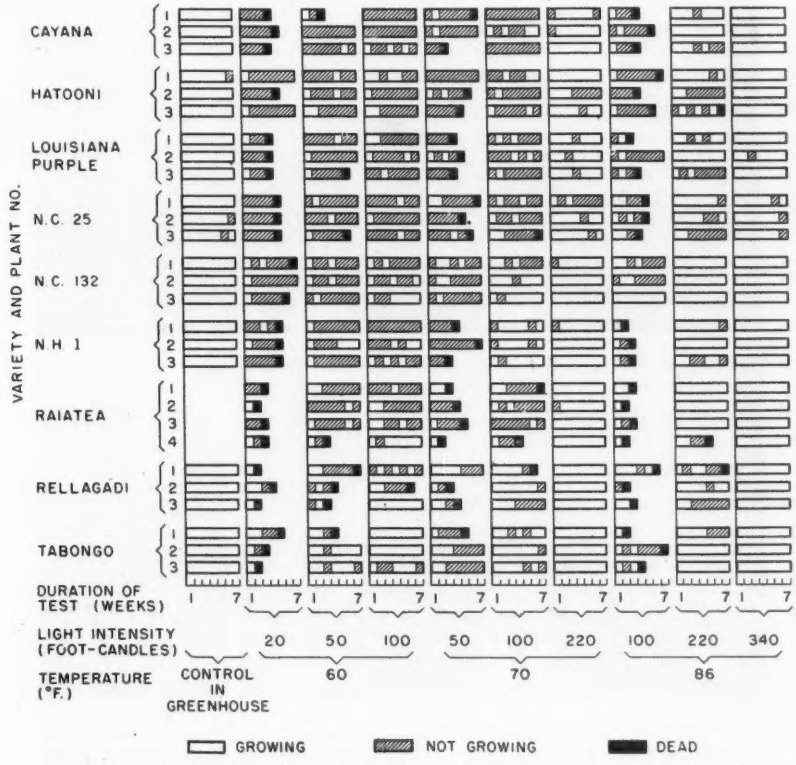

FIGURE 4.—Response of different varieties of sugarcane and erianthus to light intensities at different temperatures in experiment 3.

mal; whereas at 70°, 78°, and 86°, and particularly at the last two temperatures, they showed symptoms of poor health, and in many cases died. The symptoms of poor health consisted of yellowing and dying of the leaves and chlorosis of the spindle,[3] particularly from ½ to 2 inches just above the upper leaf sheath. This tissue was often brittle and weak, and in many instances it collapsed and the top of the

[3] Unfurled, immature leaves.

plant fell over before death ensued. Similar symptoms were evident at the lower light intensities at 60°, 65°, and 70°.

The average total increases in height per plant of the mother stalks and mother stalks plus suckers in experiments 1 to 4 are given in tables 3 and 4.

As measured by the increase in height of mother stalks alone or of mother stalks plus suckers, most varieties showed an increase in growth with an increase in light intensity at all temperatures. The sums of the total increase in height of individual varieties showed a definite correlation with the light intensities employed at each tem-

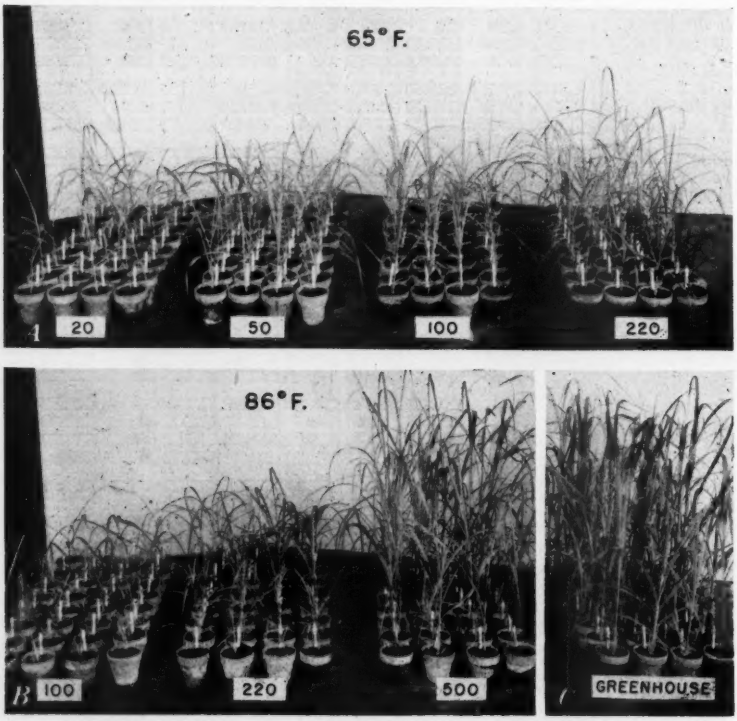

FIGURE 5.—Plants of different varieties of sugarcane grown at 65° F. (*A*), at 86° (*B*), and in a greenhouse (*C*). The numbers below the pots are foot-candles. Note how much larger the plants at 100 foot-candles are at the lower temperature; there was comparatively little difference in the size of those at 220 foot-candles. The temperature generally ranged from 75° to 85° in the greenhouse, where no light-intensity measurements were made. The varieties were Caña Criolla, Co. 281, C. P. 1165, C. P. 29/291, C. P. 31/294, C. P. 31/511, C. P. 34/79, Djatiroto, N. C. 117, and P. O. J. 2725.

perature. It is obvious that the age of the plants affected their rate of growth as well as their survival; that is, rate of growth under the same light intensities was greater in the older plants in experiments 1 and 2 than in the younger plants in experiments 3 and 4.

At a light intensity of 100 foot-candles there was less total growth in all instances (sum of totals of individual varieties) at 78° and at 86°

than at 70° F., and in some instances less than at 60° (table 3). Growth was greater at 70° than at 60°. There was also more injury to the plants at 78° and 86° than at 70°. The results indicate that more light is required for health at 78° and 86° than at 60° and 70°. At a light intensity of 50 foot-candles the total growth was sometimes greater at 60° and sometimes at 70°.

TABLE 4.—*Total average increase in height per plant of mother stalks plus suckers and of mother stalks alone of different varieties of sugarcane exposed to various conditions of light and temperature during 4 weeks,*[1] *in experiment 4*

MOTHER STALKS PLUS SUCKERS

Variety	Average initial height of mother stalk	Increase in height with indicated light intensity (foot-candles) at—							Greenhouse controls
		65° F.				86° F.			
		20	50	100	220	100	220	500	
	Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*
Caña Criolla	8.3	0.3	0.7	0.8	2.0	2.0	2.5	8.7	38.5
Co. 281	13.1	.1	.8	.8	1.9	1.6	4.3	17.5	28.8
C.P. 1165	12.8	.8	.8	3.7	6.2	1.5	2.3	19.2	39.7
C.P. 29/291	14.7	1.5	1.4	1.9	4.1	2.0	4.0	18.4	29.6
C.P. 31/294	14.6	.7	.5	1.5	4.3	2.0	5.8	20.3	31.2
C.P. 31/511	12.1	1.2	1.8	1.8	3.3	1.8	5.5	20.0	25.2
C.P. 34/79	11.9	.3	.7	.8	2.2	1.0	.3	12.2	24.2
Djatiroto	13.5	.7	1.0	1.8	6.3	2.5	6.8	30.0	51.3
N.C. 117	8.5	.3	.7	.3	.7	2.3	3.7	7.8	14.2
P.O.J. 2725	11.8	.7	.8	.3	.8	1.3	1.3	12.5	16.7
Total		6.6	9.2	13.7	31.8	18.0	36.5	166.6	299.4

MOTHER STALKS ALONE

Caña Criolla	8.3	0.2	0.7	0.8	2.0	1.8	2.5	7.2	9.2
Co. 281	13.1	.1	.8	.8	1.9	1.6	4.3	16.3	18.5
C.P. 1165	12.8	.5	.5	1.0	5.8	1.2	2.2	18.8	18.0
C.P. 29/291	14.7	1.3	1.4	1.9	4.1	2.0	4.0	18.3	25.5
C.P. 31/294	14.6	.7	.5	1.5	4.3	2.0	5.8	20.2	23.2
C.P. 31/511	12.1	1.2	1.8	1.8	3.3	1.8	5.5	20.0	19.7
C.P. 34/79	11.9	.3	.7	.8	2.2	1.0	.2	11.8	15.0
Djatiroto	13.5	.3	.8	1.8	5.7	1.5	4.8	23.7	23.7
N.C. 117	8.5	.3	.7	.3	.7	2.3	3.7	7.8	11.8
P.O.J. 2725	11.8	.7	.7	.3	.8	1.3	1.3	12.5	16.7
Total		5.6	8.6	11.0	30.8	16.5	34.3	156.6	181.3

[1] Period covered was June 13 to July 11, 1941. The plants were 64 days old when the experiment was started.

In view of the fact that growth was limited as much at 70° as at 60° F. at a light intensity of 50 foot-candles, it would seem that a light intensity between 20 and 50 foot-candles might be found that would limit growth more at 70° than at 60°.

There was considerable difference in the total growth of varieties grown at the various light intensities at the different temperatures. Some of this difference was related to the size of the plants at the beginning of the experiments. Particularly was this true in experiments 1 and 2. Three factors may have entered actively into this relation. (1) Under uniform conditions in a greenhouse certain varieties grew faster than others, indicating a normal differential rate of growth among varieties. A similar differential rate of growth might be expected among varieties when exposed to different conditions of light and temperature. (2) The difference in height of plants of different varieties at the beginning of an experiment may have

influenced varietal rate of growth. The taller varieties were near the source of light and, therefore, were exposed to higher light intensities than the shorter ones. (3) In some instances, the rate of growth was influenced by the number of suckers present at the beginning of the experiments. Conditions in the greenhouse were much more conducive to suckering than the different conditions of light and temperature used in these experiments. In experiments 3 and 4 the plants of different varieties were more nearly the same size when exposed to the various light intensities and temperatures than those in experiments 1 and 2, yet considerable varietal difference in behavior was evident after exposure. The results of experiments 1 and 2 indicate strongly that some of the varieties behaved differently under the environmental conditions of these experiments. That there is a varietal response is indicated by the results obtained with Louisiana Purple and Rellagadi in experiment 3. Louisiana Purple showed little growth at any of the combinations of light and temperature, whereas Rellagadi showed more growth at all combinations and a great deal more at some, although the plants were smaller than Louisiana Purple at the beginning of the experiment. Similar differences in rate of growth were obtained with these two varieties in experiment 1.

TABLE 5.—*Average growth increment per plant of mother stalks plus suckers of different varieties of sugarcane and erianthus exposed for various periods to different conditions of light and temperature in experiment 2*

Variety	Temperature	Light intensity	Growth increment after indicated period (weeks)							Total
			1	2	3	4	5	6	7	
	°F.	*Foot-candles*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*
	60	20	0.8	0.5	0.8	0	0.3	[1] 0	0.3	2.7
		50	2.3	1.3	2.0	2.5	3.3	2.3	1.8	15.5
		100	3.5	2.5	2.0	2.3	2.0	1.5	.8	14.6
	70	50	3.5	2.3	0	0	0	0	0	5.8
Burma		100	1.8	2.3	1.5	3.3	1.8	0	.3	11.0
		220	1.8	3.8	.5	2.8	6.5	5.0	3.5	23.9
	86	100	2.5	.5	[1] 0	0	0	0	(2)	3.0
		220	6.0	2.5	3.5	7.8	3.0	.8	5.5	29.1
		340	5.8	4.8	5.3	12.5	8.3	13.0	12.3	62.0
	60	20	.5	0	0	0	0	0	[3] 0	.5
		50	0	0	0	.3	.2	.2	.5	1.2
		100	.2	0	.8	.8	1.3	.5	.5	4.1
	70	50	.2	.7	.3	.5	0	[1] 0	.7	2.4
Cayana		100	.7	.7	.2	0	0	.8	.5	2.9
		220	1.0	.8	1.0	.5	1.2	1.5	1.7	7.7
	86	100	.3	.3	2.0	2.2	1.3	2.0	[4] .7	8.8
		220	1.7	1.3	.5	2.5	1.3	3.0	3.3	13.6
		340	2.8	2.5	6.8	5.0	6.7	9.5	6.5	39.8
	60	20	.5	0	0	0	0	0	[1] 0	.5
		50	.8	0	.2	0	.3	.2	0	1.5
		100	0	.5	.2	.3	.2	.2	0	1.4
	70	50	.8	0	0	0	0	0	0	.8
Hatooni		100	.5	0	0	.3	0	.2	.5	1.5
		220	.7	.5	.3	.5	.3	1.0	1.3	4.6
	86	100	.8	0	0	[1] 0	[2] 0	(2)	----	.8
		220	1.0	.5	.3	.5	4.2	4.0	4.8	15.3
		340	1.5	2.0	2.2	1.2	1.5	2.2	1.7	12.3
	60	20	.2	.2	0	[1] 0	(2)	----	----	.4
		50	1.0	0	.2	0	.2	0	.2	1.6
		100	0	0	0	0	0	0	0	0
	70	50	.3	0	0	0	(2)	----	----	.3
Louisiana Purple		100	.3	.3	.3	.2	0	0	0	1.1
		220	.2	.3	0	.2	0	0	0	.7
	86	100	.5	.2	0	[1] 0	[3] 0	(2)	----	.7
		220	1.0	.8	.3	.2	.2	.2	.3	3.0
		340	.5	.5	.8	1.5	.8	.3	.3	4.7

See footnotes at end of table.

TABLE 5.—*Average growth increment per plant of mother stalks plus suckers of different varieties of sugarcane and erianthus exposed for various periods to different conditions of light and temperature in experiment 2*—Continued

Variety	Temperature	Light intensity	Growth increment after indicated period (weeks)							Total
			1	2	3	4	5	6	7	
	°F.	*Foot-candles*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*
	60	20	0.3	0	0	[1] 0	[2]			0.3
		50	0	0	.2	0	0	0	0	.2
		100	.2	.2	0	0	.3	0	0	.7
N.C. 25	70	50	.5	.2	0	0	.2	[1] 0	0	.9
		100	0	.2	0	0	0	0	0	.2
		220	.2	0	.5	.5	.2	.2	.2	1.8
	86	100	.2	.2	0	0	[2]			.4
		220	.3	1.7	.5	1.0	.5	1.3	2.3	7.6
		340	.7	2.3	1.7	1.3	0	0	0	6.0
	60	20	.7	.2	0	.2	.2	0	0	1.3
		50	.8	.3	1.0	1.3	1.0	1.5	1.5	7.4
		100	.5	.8	1.8	2.0	2.0	2.5	1.7	11.3
N.C. 132	70	50	2.2	1.0	1.3	1.8	2.3	1.8	.5	10.9
		100	.5	.3	.7	1.5	3.5	2.0	2.5	11.0
		220	1.3	2.2	2.7	2.8	3.0	3.2	3.5	18.7
	86	100	3.0	.7	1.2	.5	2.2	2.8	.7	11.1
		220	3.0	3.0	4.0	7.2	5.0	3.7	5.0	30.9
		340	2.3	3.7	5.3	6.2	5.8	6.3	6.0	35.6
	60	20	2.0	.3	.2	.2	.3	.2	[3] 0	3.2
		50	1.2	1.0	1.0	.8	1.0	.3	.5	5.8
		100	1.3	.8	2.0	2.3	2.0	2.0	1.5	11.9
		50	4.2	1.3	.8	1.0	.5	0	.5	8.3
N.H. 1	70	100	3.3	2.5	1.8	1.8	1.8	2.3	3.3	16.8
		220	4.0	2.7	2.7	3.8	3.8	3.7	4.5	25.2
		100	5.7	.7	.5	.2	.2	[3]	[2]	7.3
	86	220	6.0	6.0	5.8	8.0	6.7	4.2	5.3	42.0
		340	5.3	7.0	5.8	7.8	7.2	6.7	6.7	46.5
		20	1.3	.2	[1] .2	0	[3] 0	0	[2]	1.7
	60	50	1.2	.7	1.0	1.3	1.2	.8	.8	7.0
		100	1.3	1.2	1.5	1.7	2.3	3.0	2.8	13.8
		50	3.5	3.5	2.0	.8	0	0	1.2	11.0
Pasoeroean	70	100	2.8	3.7	3.7	3.3	2.7	2.2	2.3	20.7
		220	4.0	6.7	6.0	6.0	5.5	5.8	8.5	42.5
		100	5.5	1.5	.8	1.8	[1] 2.5	4.5	.8	17.4
	86	220	8.3	11.8	11.3	[4] 0.8	13.2	9.5	7.0	71.9
		340	7.2	14.0	13.2	13.2	17.2	10.8	13.7	89.3
	60	20	1.0	.2	0	[1] 0	[3] 0	0	[2]	1.2
		50	.5	.2	0	.5	.2	.2	0	1.6
		100	.7	.5	.2	.8	.7	.5	.5	3.9
		50	2.5	.5	.3	.3	[1] .2	0	.2	4.0
Raiatea	70	100	1.5	.5	.8	.8	1.8	2.7	3.5	11.6
		220	1.2	1.3	1.8	2.7	4.5	4.7	5.2	21.4
		100	1.7	.3	.5	.3	[1] .2	.2	0	3.2
	86	220	3.8	3.2	4.8	5.8	5.2	3.2	4.8	30.8
		340	4.0	6.3	9.5	10.0	7.8	7.8	7.7	53.1
		20	2.0	.8	0	0	.2	0	.2	3.2
	60	50	2.3	1.8	1.0	.7	.5	1.5	1.7	9.5
		100	2.8	1.7	2.0	1.3	2.8	2.3	2.5	15.4
		50	5.0	3.3	4.2	1.8	1.5	.8	1.2	17.8
Tabongo	70	100	5.5	5.3	2.7	3.0	4.2	4.2	3.2	28.1
		220	4.8	7.2	6.3	4.5	7.8	5.3	7.5	43.4
		100	6.2	5.5	3.8	4.5	5.2	3.5	1.7	30.4
	86	220	10.0	11.8	11.3	6.8	10.7	12.7	15.2	78.5
		340	12.0	18.5	12.5	16.3	21.5	14.5	14.2	109.5
	60	20	0	0	[1] 0	[3] .2	0	0	0	.2
		50	2.0	0	[1] 0	.2	.2	0	0	2.4
		100	.2	0	0	0	0	.5	0	.7
		50	1.2	0	0	0	0	.2	0	1.4
U.S. 4515	70	100	.2	.2	0	.2	0	0	0	.6
		220	1.7	.3	0	1.0	.8	.8	.7	5.3
		100	.2	.5	0	.3	0	0	0	1.0
	86	220	.3	.3	.2	.3	0	0	0	1.1
		340	1.7	.5	.3	.3	0	0	.8	3.6

[1] 1 plant dead.
[2] All plants dead.
[3] 2 plants dead.
[4] Growth due to suckers; mother stalks dead.

The rate and change of rate of growth of the varieties in experiment 2 (table 5) serve to differentiate clearly not only the effects of temperature and light intensity but also varietal behavior. Very little

growth occurred in Hatooni, and even less in N.C. 25, Louisiana Purple, and U.S. 4515, as compared with other varieties at most of the conditions of light and temperature. In the varieties that showed considerable growth there was a tendency for the rate of growth at low light intensity at each of the temperatures to decline with the lapse of time. This decline was sometimes more marked at the higher temperatures, although the low light intensity was higher at the higher temperatures than at the low. On the other hand, at the higher intensities at all the temperatures, and particularly at the higher temperatures, the initial rate of growth was more often maintained and in some instances increased during the succeeding periods of exposure. At least part of this more favorable response at the higher temperatures can be attributed to the higher light intensities employed as compared with those at the lower temperatures. At low intensities of light the rate of growth tended to be higher during the first week than during the later weeks of exposure. This tendency was apparent at many of the intensities in varieties that showed little growth at any of the conditions of light and temperature. It is possible that the preceding conditions of growth in the greenhouse may have had some effect upon this initial period under experimental conditions.

In experiment 5 (table 6) one plant each of two varieties was exposed to light intensities of 200 and 1,750 foot-candles at 86° F. for 4 weeks. It will be seen that the higher intensity (1,750 foot-candles) was much more favorable for growth than the light intensities used in the other experiments (1 to 4). None of the experiments, of course, was designed to determine the optimum light intensity; nor is it definitely known whether the optimum light for the growth of sugarcane is ever exceeded in nature. Clements (*3*) has shown, however, that under natural conditions light intensity may become too low for maximum growth.

TABLE 6.—*Growth increments in plants (mother stalks plus suckers) of 2 varieties of sugarcane exposed for 4 weeks*[1] *to 2 light intensities at 86° F. and a relative humidity of about 75 percent, experiment 5*

Variety	Light intensity	Initial height of mother stalk	Growth increment after indicated period (weeks)				Total increase in length	Dry weight
			1	2	3	4		
	Foot-candles	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Gm.*
Burma	200	10	4.5	0.5	6.0	2.5	13.5	1.2
	1,750	12	16.5	51.5	76.5	56.5	201.0	20.3
Cayana	200	21	5.0	3.0	10.5	5.5	24.0	4.7
	1,750	19	18.5	25.0	23.5	19.0	86.0	40.2

[1] The period covered was Jan. 10 to Feb. 7, 1941. The plants were 94 days old at the beginning of the experiment.

Tables 7 and 8 show the average dry weights of plants at the different conditions of light and temperature obtained in experiments 1 to 4. In addition to these data, dry weights of control plants grown in the greenhouse in connection with experiments 3 and 4 are shown in tables 7 and 8. The initial weights of plants representative of those exposed to the various conditions of light and temperature in experiment 4 are given in table 8.

TABLE 7.—*Average dry weight of plants of different varieties of sugarcane and erianthus exposed for 7 weeks to various conditions of light and temperature in 3 experiments*

Experiment and variety	Dry weight with indicated light intensity (foot-candles) at—									
	60° F.			70° F.			78° or 86° F.[1]			Greenhouse controls
	20	50	100	50	100	220	100	220	340	
Experiment 1:	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*
Burma	12.4	14.1	11.7	15.6	12.4	21.3	15.3	16.9	20.3	.....
Cayana	6.6	6.7	10.0	6.0	10.6	12.2	8.1	11.3	26.0	.....
Gehra Bon	5.4	7.5	8.4	4.8	4.4	7.4	4.9	7.2	9.1	.....
Hatooni	7.2	8.3	11.7	5.8	9.3	10.8	9.0	10.2	11.7	.....
Louisiana Purple	[2] 7.0	7.0	7.7	7.0	7.9	8.0	5.0	9.9	12.0	.....
N. C. 132	[2] 5.8	7.5	6.0	5.8	6.2	8.0	5.3	9.2	15.1	.....
N. H. 1	8.9	8.1	13.8	10.8	14.9	15.1	11.5	14.5	23.2	.....
Pasoeroean	8.6	12.0	14.2	6.9	7.4	9.3	10.3	14.9	17.8	.....
Rellagadi	12.4	14.2	15.4	9.8	12.0	17.4	11.4	15.6	19.3	.....
Tabongo	10.4	13.7	14.1	10.9	13.3	17.8	12.2	15.5	21.1	.....
28 N. G. 7	5.5	8.1	8.3	5.2	5.1	10.5	5.7	9.2	16.8	.....
Total	90.2	107.2	121.3	88.6	103.5	137.8	98.7	134.4	192.4	.....
Experiment 2:										
Burma	2.3	3.8	2.2	2.1	2.2	2.5	1.9	4.0	5.6	.....
Cayana	3.4	4.0	3.9	4.0	4.0	5.1	3.5	4.3	9.3	.....
Hatooni	2.6	3.1	3.6	3.0	3.9	4.8	2.4	4.4	8.4	.....
Louisiana Purple	3.3	3.2	2.4	2.3	3.0	3.0	1.7	2.8	4.9	.....
N. C. 25	3.9	3.8	4.1	4.4	2.4	3.2	2.1	3.7	7.6	.....
N. C. 132	4.7	4.9	4.7	4.3	3.2	4.2	3.1	4.4	7.0	.....
N. H. 1	6.3	6.8	7.9	6.7	6.7	7.7	5.0	9.9	11.8	.....
Pasoeroean	4.2	4.7	4.6	3.9	4.3	6.1	4.2	6.3	7.7	.....
Raiatea	3.8	4.3	4.3	4.1	5.1	5.7	3.3	7.8	11.2	.....
Tabongo	4.6	6.1	6.5	5.6	5.4	6.7	5.9	5.7	9.6	.....
U. S. 4515	3.0	1.9	2.6	2.8	2.3	2.6	2.5	2.7	2.4	.....
Total	42.1	46.6	46.8	43.2	42.5	51.6	35.6	56.0	85.5	.....
Experiment 3:										
Cayana	2.5	3.5	.1	3.1	3.5	3.2	2.1	3.8	6.0	22.3
Hatooni	4.8	4.7	5.5	3.6	4.3	6.7	3.7	5.5	11.1	34.3
Louisiana Purple	1.9	1.9	2.1	1.9	2.3	3.9	2.9	5.2	6.8	28.5
N. C. 25	2.3	2.3	1.7	2.2	2.4	4.0	2.6	4.4	5.6	21.0
N. C. 132	1.2	1.6	1.5	1.3	2.9	2.4	2.4	2.8	3.5	17.0
N. H. 1	2.5	3.0	1.9	1.7	2.8	5.7	2.9	3.2	6.4	28.1
Raiatea	2.8	2.5	2.7	2.5	2.2	3.5	1.9	3.6	5.2	.....
Rellagadi	1.5	2.0	1.5	1.9	1.4	2.6	1.3	1.4	2.9	31.0
Tabongo	1.2	2.1	1.9	1.9	1.9	3.0	1.4	2.5	3.6	20.2
Total	20.7	23.6	21.9	20.1	23.7	35.0	21.2	32.4	51.1	202.4

[1] 78° in experiment 1 and 86° in experiments 2 and 3.

[2] There were no plants of Louisiana Purple and N. C. 132 at 20 foot-candles at 60° F. in experiment 1. Because the dry-weight values of these varieties were similar to those at 20 foot-candles at 60° and at 50 foot-candles at 70° (experiments 2 and 3), the dry-weight values of these varieties (Louisiana Purple, 7 gm.; N. C. 132, 5.8 gm.) in this experiment were used in computing the total dry weight at 20 foot-candles at 60°.

In experiment 1 the relation between light intensity at each temperature is clearly seen in connection with most varieties, the dry weights increasing with the intensity of the light. This relation holds at 86° F. in experiment 2 (table 7). At 70° in experiment 2 the tendency for the dry weights to increase with the light intensities is offset by exceptions. However, in most instances the dry weights are higher at the highest light intensity than at the two lower intensities. At 60° (table 7, experiment 2) the dry weights at the two highest intensities are in some instances slightly greater than at the lowest, but the difference is not marked. In experiment 3 (table 7) there appears to be no relation between dry weights and light intensity at 60°; at 70° there appears to be a relation in some varieties, and at 86° the correlation is clear. In experiment 4 (table 8) the three lowest light intensities at 65° seem to have little or no effect on dry weight. The highest light intensity at this temperature seems

to have caused an increase in dry weight in some varieties. At 86° the dry weights increased with the light intensity. In general, although not as conclusively as the growth increments (increase in length of stalk), dry weight indicates a dependence on light intensity for its production. At the higher temperatures this relation is clear. At the lower temperatures, which themselves become a limiting factor, the effect of light intensity is often not evident. However, the higher light intensities maintain a much better condition of health in the plants at each of the temperatures than the lower light intensities. The dry-weight data in these experiments indicate that the low light intensities (50 and 100 foot-candles) at 78°, 86°, and 70° are no more favorable, and in some instances apparently less favorable, to the production of dry matter than these same light intensities at 60°, although these higher temperatures are normally much more favorable to growth than the lower ones.

TABLE 8.—*Average initial dry weights and average dry weights of plants of different varieties of sugarcane exposed for 4 weeks to various conditions of light and temperature; experiment 4*

Variety	Initial dry weight	Dry weight with indicated light intensity (foot-candles) at—							Greenhouse controls
		65° F.				86° F.			
		20	50	100	220	100	220	500	
	Gm.	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*	*Gm.*
Caña Criolla	1.5	1.7	1.6	1.6	1.9	1.4	1.8	3.3	10.6
Co. 281	2.5	2.2	2.5	1.9	2.3	2.5	2.2	5.7	11.3
C. P. 1165	2.7	3.0	2.5	3.6	4.1	2.9	3.6	6.3	13.5
C. P. 29/291	2.3	2.6	2.2	2.8	3.3	2.5	3.3	5.7	15.0
C. P. 31/294	2.2	1.8	2.4	2.1	3.2	2.4	2.7	5.6	13.3
C. P. 31/511	3.2	2.7	3.0	2.5	3.8	2.8	3.8	5.8	14.4
C. P. 34/79	2.4	2.3	2.9	2.7	3.9	2.6	3.4	7.0	12.2
Djatiroto	2.2	1.6	1.7	1.9	1.9	1.8	2.0	4.8	11.0
N. C. 117	1.2	1.1	1.6	1.1	1.6	1.3	1.7	2.9	9.2
P. O. J. 2725	2.5	2.2	2.8	2.5	2.8	2.6	2.6	7.4	13.6
Total	22.7	21.2	23.2	22.7	28.8	22.8	27.1	54.5	124.1

In the foregoing experiments the growth response of the several varieties to the light-temperature combinations employed seemed to bear no relation to the latitudes in which the varieties originated, but this may be attributable to limitations of the environmental factors artificially set up, especially the deficiency of light in most experiments. Field observations strongly hint that at relatively low temperatures the northern varieties respond to the stimulus of adequate light (daylight at Arlington Experiment Farm, Arlington, Va.) and grow faster than equatorial varieties. In the experiments under consideration, however, Louisiana Purple, coming from latitude 6° S., behaved similarly in its growth response to U. S. 4515, originating at latitude 40° N. Both varieties showed little growth under any of the environmental conditions. The noble canes (Louisiana Purple, Caña Criolla, N.C. 25, and N.C. 117), varying in their origin from latitude 6° S. to 11° and 21° N., showed relatively little growth at any of the combinations of light and temperature.

DISCUSSION

The minimum light requirement for health and growth of sugarcane in the experiments here reported may have been conditioned only by

the compensation point between the anabolism of photosynthesis and the catabolism of respiration. If the destruction was greater than the synthesis of carbohydrates, the plants suffered starvation as a result of a shortage of this type of food. It is possible, however, that the plants may have suffered injury as a result of direct or indirect effects of limiting light intensities on such factors as other phases of nutrition, absorption of solutes, and transpiration, even when the amount of carbohydrates in the plants exceeded that required in respiration.

The results of studies by McLean (*5*), Yap (*7*), and Gooding (*4*) indicate the possibility that light intensity may become too great during midday in the Philippine Islands and in Barbados, British West Indies, for the maximum rate of photosynthesis in sugarcane. The results of McLean obtained in the Philippines showed a maximum rate of photosynthesis during the morning between 7:30 and 9:30 and in the afternoon between 3:30 and 5:30 (*5*). Yap, working in the Philippines, found the maximum rate of photosynthesis between 8 and 10 a. m., a depression between 10 a. m. and 2 p. m., and an increase between 2 and 4 p. m. It is possible, and perhaps probable, that the midday depression of the rate of photosynthesis was the result of indirect effects such as those produced by high temperatures and disturbed moisture relations. Yap noted that during the midday period there was a rolling of the tips of the leaves. He also reported greater photosynthetic activity in young leaves, and a decreasing rate with age.

Singh and Lal (*6*), working in India with severed leaves of the Reori variety of sugarcane at a temperature of 30° C. (86° F.) and with a normal carbon dioxide content of the air, found an increase in the rate of photosynthesis with an increase in light intensity from 90 to 1,875 foot-candles, the highest intensity used. At an atmospheric concentration of carbon dioxide and a light intensity of 1,875 foot-candles, there was an increase in the rate of photosynthesis with a rise in temperature from 23° C. (73.4° F.) to 30° C. (86° F.) and an initial increase in rate with a rise from 30° C. to 34° C. (93.2° F.), followed by a decline in rate at 34°.

The different responses of the varieties and species of sugarcane to minimum light requirements imply considerable practical significance, especially if there should prove to be different responses at higher light intensities to various temperatures. Such varietal differences would provide the basis for considerable adaptation to a particular climate through breeding and selection.

SUMMARY

The data here presented deal with the effects of different but relatively low light intensities, at temperatures of 60°, 65°, 70°, 78°, and 86° F., on the health, growth, and survival of plants of 21 varieties of sugarcane and 3 varieties of erianthus.

There was a varietal response to the conditions of light and temperature.

In general, the health of the plants improved and growth increased with an increase in light intensity at each of the temperatures.

For each temperature there was a minimum light intensity for survival, health, and growth; the higher the temperature the higher

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that minimum became. With an increase in light intensity up to approximately 220 foot-candles at 65°, and to 1,750 foot-candles at 86°, there was increased growth. At 60° and a light intensity of approximately 100 foot-candles the anabolic and catabolic processes approached a balance and the plants remained in fairly good health for 7 weeks, whereas under this same light intensity at 78° and 86°, particularly at 86°, the life of the plants was impaired and death was common.

These data suggest that, for every temperature within the normal range of temperatures occurring naturally, a definite quota of light is required for maximum growth.

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THE ARGENTINE CURLY TOP OF SUGAR BEET[1]

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INTRODUCTION

In 1925 Fawcett (*8*)[2] described a disease, called encrespamiento, of sugar beets (*Beta vulgaris* L.) in the Province of Tucumán, Argentina. He reported that it produced symptoms indistinguishable from those caused by curly top of sugar beets in the western part of the United States. However, Fawcett (*9, 10*), Henderson (*16*), and Severin and Henderson (*20*) were unable to find *Eutettix tenellus* (Bak.), the vector of the virus of North American curly top, in Argentina. Fawcett showed that the vector of the Argentine curly top virus is a leafhopper that at different times has been identified as *Aceratogallia sanguinolenta* (Prov.) (*8*) and (*Agallia*) *Agalliana sticticollis* (Stål.) (*10*). This leafhopper has been described more recently by Oman (*18*) as a distinct species, *Agalliana ensigera*.

Curly top is extremely destructive to sugar beets and other crops in the western part of the United States. Until the introduction of curly-top-resistant varieties almost complete abandonment of the sugar-beet industry in several of the Western States was threatened because of this disease.

Because of the similarity of the Argentine disease to North American curly top and its potential economic significance if introduced into the sugar-beet-producing areas of other parts of the world, the disease has been of considerable interest to the sugar-beet industry of the United States. At different times efforts have been made to obtain additional information regarding it through direct studies of diseased material. On two occasions, in 1927 and again in 1937, diseased plants were obtained from Tucumán and by special arrangement with the plant-quarantine authorities were brought to Washington, D. C., for study and comparison with North American curly top in quarantine greenhouses. In the season of 1940–41 further studies of the disease were made by the senior author at the Estación Experimental Agrícola de Tucumán in Argentina. The results of all these studies are presented in this paper.

[1] Received for publication May 31, 1944.

[2] Italic numbers in parentheses refer to Literature Cited, p. 47.

COMPARISON OF SYMPTOMS AND TRANSMISSIBILITY OF ARGENTINE AND NORTH AMERICAN CURLY TOP [3]

In 1927 plants [4] of sugar beet and chard (*Beta vulgaris* var. *cicla* L.) affected with curly top were brought from Tucumán, Argentina, to Washington, D. C., and placed in a quarantine greenhouse at the Arlington Experiment Farm, Arlington, Va., for study in comparison with North American curly top. New growth from both kinds of plants showed leaf curling, veinlet clearing, and vein swelling indistinguishable from the symptoms that characterize the curly top disease in the United States. Drops of exudate were observed on badly diseased petioles of both the sugar-beet and the chard plants similar to those found on petioles of sugar-beet plants affected with North American curly top. Transverse sections of badly affected petioles showed vascular necrosis. Symptoms of Argentine curly top, in comparison with those of North American curly top, are illustrated in figures 1 and 2.

Tests were made in which nonviruliferous beet leafhoppers (*Eutettix tenellus*) were caged for different periods on the diseased sugar-beet and chard plants received from Argentina and were later transferred to small sugar-beet plants. As shown in table 1, where the results of these tests are summarized, no infection was obtained, although a high percentage of the check plants on which leafhoppers from plants affected with North American curly top were caged became infected. Plants from one of these tests, illustrating the results obtained with leafhoppers that had fed on diseased Argentine and North American plants, respectively, are shown in figure 3.

A transmission test with an aphid thought to be *Myzus persicae* (Sulz.) also gave negative results.

In 1937 a second lot of diseased plants, consisting of the sugar-beet variety U. S. 12 and the mangel-wurzel (*Beta vulgaris*) varieties Yellow Tankard and Red Mammoth, was obtained from Argentina through the courtesy of G. L. Fawcett, for further experimental work in the quarantine greenhouse at Arlington, Va. These plants showed all the symptoms typical of curly top in the United States, such as leaf curling, veinlet clearing, vein swelling, and production of exudate on diseased petioles, that had been observed on plants of the 1927 importation.

TABLE 1.—*Results of attempts to transmit North American curly top and Argentine curly top to sugar beet by means of Eutettix tenellus in quarantine greenhouse, Arlington, Va., 1927 and 1937–39*

Year	Disease affecting plants on which the beet leafhoppers fed	Plants inoculated by means of beet leafhoppers	Plants infected	
		Number	*Number*	*Percent*
1927	North American curly top	18	15	83.3
	Argentine curly top	34	0	0
1937–39	North American curly top	80	46	57.5
	Argentine curly top	127	0	0

[3] Experimental work performed by Eubanks Carsner, G. H. Coons, and E. W. Brandes.

[4] These plants were obtained from G. L. Fawcett, of the Estación Experimental Agrícola de Tucumán, and were brought to Washington through the courtesy of C. F. Henderson, of the Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture.

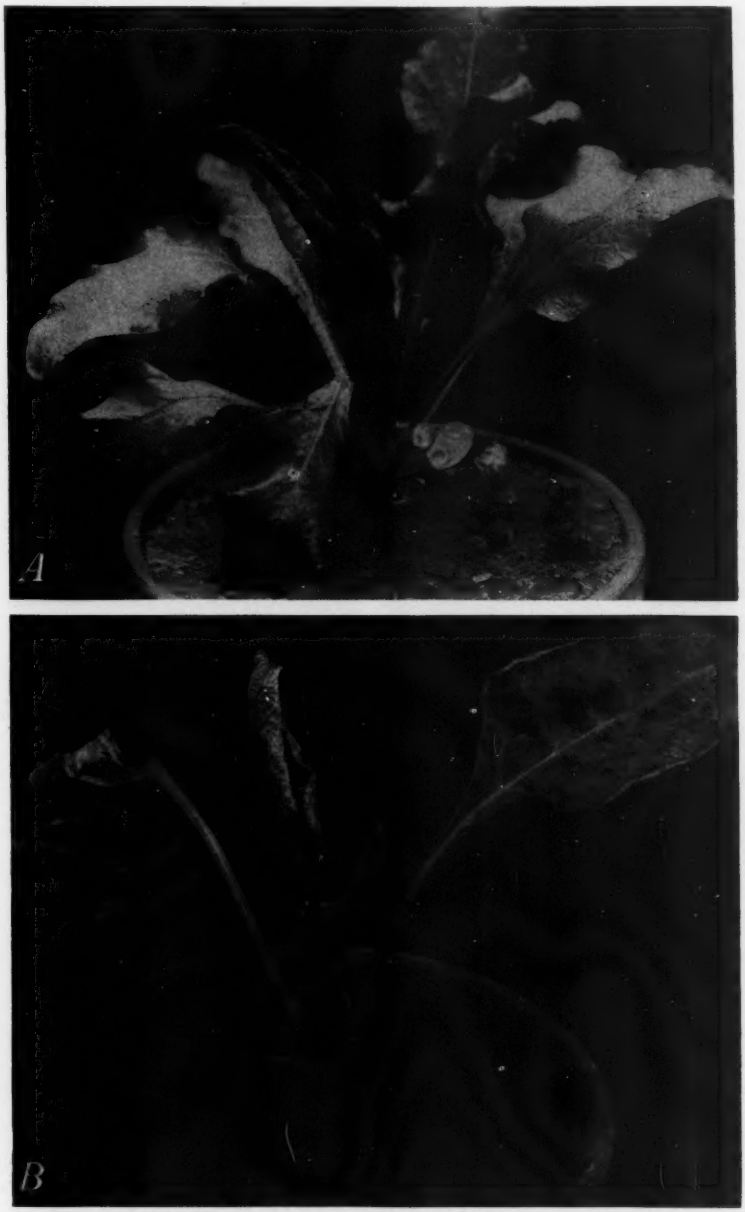

FIGURE 1.—*A*, Sugar-beet plant affected with Argentine curly top, showing typical leaf curling, vein swelling, and roughened under side of leaves; photographed at Arlington, Va., 1927. *B*, Sugar-beet plant affected with North American curly top, showing typical symptoms of this disease; photographed at Riverside, Calif., 1943.

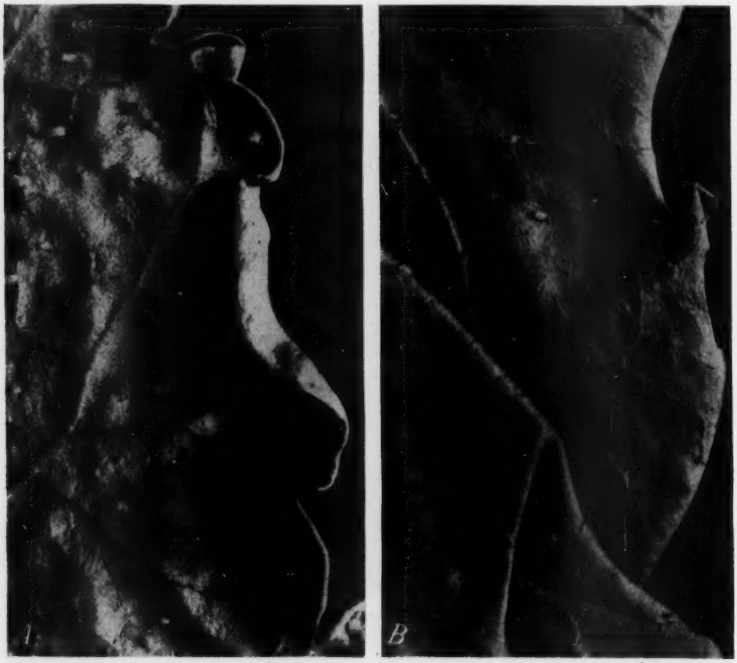

FIGURE 2.—Vein protuberances on under side of leaves of sugar-beet plants affected with (*A*) Argentine curly top and (*B*) North American curly top; number and distribution of papillae are probably not distinctive characteristics. Photographed at Arlington, Va., 1927; × about 5.

FIGURE 3.—*A*, Sugar-beet plants to which beet leafhoppers (*Eutettix tenellus*) were transferred from diseased Argentine plants; *B*, sugar-beet plants to which beet leafhoppers were transferred from diseased North American plants. Only North American curly top was transmitted by the beet leafhoppers. Photographed at Arlington, Va., November 29, 1927.

This material was used in further attempts to obtain transmission of the Argentine curly top virus by means of the beet leafhopper. Parallel tests were conducted in which sugar-beet plants affected with North American curly top were the virus source. In an extensive series of tests, nonviruliferous beet leafhoppers were allowed to feed on diseased plants and later were transferred to small sugar-beet plants. The results of these tests, also summarized in table 1, are similar to those obtained earlier in that no infection by the Argentine virus was obtained, whereas the percentage of infection was relatively high on control plants inoculated by means of beet leafhoppers that had fed on plants infected with the North American virus.

Attempts were made also to transmit the Argentine virus by juice inoculation. In these tests juice was extracted from diseased beet leaves, diluted 1 part juice to 1 part water, and introduced into beet plants with about six true leaves by means of numerous punctures into the crowns. Small insect pins were used for making the punctures through drops of inoculum placed on the crowns. The 76 plants inoculated showed no infection. In a second type of test, inoculum was rubbed over the surface of the leaves on which carborundum had been sprinkled previously. The 12 plants so treated showed no infection.

In 1935 and again in 1937 dried leaves were obtained from diseased beets from Tucumán. These were ground to a powder and soaked overnight in distilled water. The liquid was extracted and added to an equal volume of 95-percent alcohol. The resulting precipitate was dried, mixed with 5-percent sugar solution to which 0.5 percent of sodium citrate was added, and fed to nonviruliferous beet leafhoppers, which were then caged singly on seedling sugar beets. Extensive tests were made from each of the two lots of leaves but no infection was obtained. With this technique the virus of North American curly top has been recovered from beet leaves after they had remained dry for 3 years (*1*).

Dried leafhoppers (*Agalliana ensigera*), sent by G. L. Fawcett from Tucumán, were used in three inoculation tests in November and December 1937. One lot of the leafhoppers had been caged on a diseased beet for more than 3 months, and another lot was collected from a field of completely diseased beets just before mailing on October 29, 1937. On November 15 and 30 and December 9, dried leafhoppers were ground in a mortar and an alcoholic precipitate was obtained. The precipitate was dried and suspended in 5-percent sugar solution. Nonviruliferous beet leafhoppers were allowed to feed on the suspension and then were caged singly on healthy young sugar beets, 88 plants being thus inoculated. None became diseased. Comparable tests by Bennett, not previously reported, with the North American curly top virus and dried beet leafhoppers have shown that the virus could be recovered from the dried insects after 3 months.

In January 1938, four sugar-beet plants, numbered 1 to 4 and known to be infected by the Argentine virus, were inoculated with North American curly top. Plant 1 died about the middle of February, but the remaining three plants were in good condition on July 10 and none showed any increase in severity of symptoms. On that date nonviruliferous beet leafhoppers were caged on these plants and later caged singly on seedling beets. Eight plants inoculated from plant 2 re-

mained healthy, but five of seven and four of six plants inoculated by means of leafhoppers from plants 3 and 4, respectively, became infected. These results show that the strain of North American virus used was superimposed on the Argentine curly top virus in at least two of the four plants inoculated.

The transmission tests conducted with the Argentine virus appear to have been extensive enough to permit the conclusion that this virus is not transmissible by *Eutettix tenellus*. The failures to obtain transmission are all the more striking because of the high percentages of infection obtained in parallel tests in which the beet leafhopper had access to virus of North American curly top. Hence, although the viruses from the two geographical areas produce symptoms that, so far as observed, are indistinguishable on sugar beets, each is associated in its geographical range with a specific leafhopper vector, and the vector of North American curly top virus is unable to transmit the Argentine virus. Whether *Agalliana ensigera* is unable to transmit North American curly top virus is not known.

THE DISEASE IN ARGENTINA [5]

GEOGRAPHIC DISTRIBUTION

In 1923 Boncquet (*4*) described curly top on small beets at San Isidro, a suburb of Buenos Aires, as occurring commonly during the season of 1916–17. He reported also that the disease was very destructive in beet plots in Colonia Alvear in western Argentina.

Fawcett (*8*) in 1925 gave a detailed description of encrespamiento, or curly top, on sugar beet in the Province of Tucumán.

In the season of 1926–27 Henderson (*16*) found beets with typical foliage symptoms of curly top in the Provinces of Tucumán, San Juan, and Mendoza and in the Territory of La Pampa, but failed to find the disease in the Territory of Río Negro. From an extensive search in the field and the study of insect collections of museums and of entomologists, no evidence was obtained of the occurrence in Argentina of *Eutettix tenellus*, the vector of curly top virus in North America.

In 1939 A. M. Offermann collected *Agalliana ensigera* on sugar beets near Conesa, Río Negro, and found that when these insects were placed on sugar beets at the Government experimental station at José C. Paz the beets developed curly top.[6]

A colony of these insects, kindly supplied by A. M. Offermann, was taken to Tucumán in September 1940 and tested on sugar-beet seedlings of the varieties R. & G. Old Type, U. S.[7] 11, U. S. 12, and S. L.[7] 68. Plants of these four varieties proved to be susceptible to infection and developed symptoms indistinguishable from those produced on the same varieties by *Agalliana ensigera* collected at Tucumán. These results indicate clearly that the virus is present in the lower Río Negro Valley. However, a careful search for the disease in

[5] Experimental work was performed by C. W. Bennett. Appreciation is expressed to Dr. Wm. E. Cross, Director of the Estación Experimental Agrícola de Tucumán, for facilities provided during the course of this work. Indebtedness to Ing. G. L. Fawcett, pathologist, Mr. Kenneth J. Hayward, entomologist, Ing. Enrique F. Schultz, subdirector and horticulturist, Ing. Isaac Manoff, chemist, and Ing. G. A. Kreibohm de la Vega, cotton specialist, is acknowledged for much valuable assistance while the work was in progress.

[6] Unpublished information communicated to C. W. Bennett by Ing. Alfredo M. Offermann, pathologist, Ministerio de Agricultura, Buenos Aires, Argentina.

[7] Varieties released for commercial use by the Bureau of Plant Industry, Soils, and Agricultural Engineering are designated as "U. S." varieties. "S. L." refers to varieties maintained at the U. S. Sugar Plant Field Laboratory at Salt Lake City, Utah.

beet plantings, from January 12 to February 3, 1941, in the valley of the lower Río Negro, revealed no infected plants, although the vector (*A. ensigera*) was found in small numbers.

There is evidence, therefore, that the disease is rather widely distributed over the larger part of Argentina north of the Río Negro. Henderson (*16*) failed to find the disease in 1928 at La Sierra, Uruguay, and inspections of extensive acreages by the senior author in this same area in February 1941 revealed no evidence of curly top.

Sugar beets are not grown commercially in the Province of Tucumán. In and near the city of Tucumán the disease was found only in the vicinity of the Estación Experimental Agrícola de Tucumán. A plot of mangel-wurzels planted in April 1940 was inoculated by G. L. Fawcett by means of viruliferous leafhoppers from stock colonies. This plot provided an excellent source of leafhoppers and virus for infection of plants in adjacent areas. Spread, however, was not extensive, and no diseased plants were found at a distance greater than one-half mile from the plot.

Search was made for curly top in a number of localities in the Province of Tucumán. Native vegetation and cultivated plants were examined at Tafí Viejo, Lules, Ingenio Concepción, Ingenio Bella Vista, and a number of places in the immediate vicinity of the city of Tucumán. In each of these places it was found that beets and other plants known to be susceptible to curly top were grown only to a limited extent. One short row of red garden beets (*Beta vulgaris*) was found north of Tafí Viejo, and another planting of about 25 plants was found south of Lules; but no curly top was observed at either place. The scarcity of types of plants on which curly top could be recognized made it difficult to obtain information regarding the distribution of the virus, and it was not possible to determine the extent to which virus is able to spread from native or escaped plants to cultivated plants under natural conditions.

HOST RANGE

Plants Infected Naturally

In Argentina curly top has been reported on sugar beet (*8*) and tomato (*Lycopersicon esculentum* Mill.) (*11*). As will be seen later, however, there is some doubt as to the identity of the tomato disease considered to be curly top.

From October 11, 1940, to February 10, 1941, curly top was found under field conditions on mangel-wurzel var. Golden Globe, red garden beet, and four varieties of sugar beet planted at the Estación Experimental Agrícola de Tucumán. The disease was found also on one plant of a species of *Physalis* and symptoms resembling those of curly top as it occurs in the United States were noted on two plants of cultivated petunia (× *Petunia hybrida* Vilm.).

No symptoms completely typical of curly top were found on tomato, although several small plots of tomatoes were abundantly exposed to infection. One plot in particular was adjacent to a plot of badly diseased mangel-wurzels, as shown in figure 4, and the vector of curly top was abundant on mangel-wurzels throughout October, November, and December, 1940. Since all the mangel-wurzels, and later a high percentage of sugar beets in an adjacent plot, had curly top, conditions for transfer of the virus from mangel-wurzel and beet to tomato

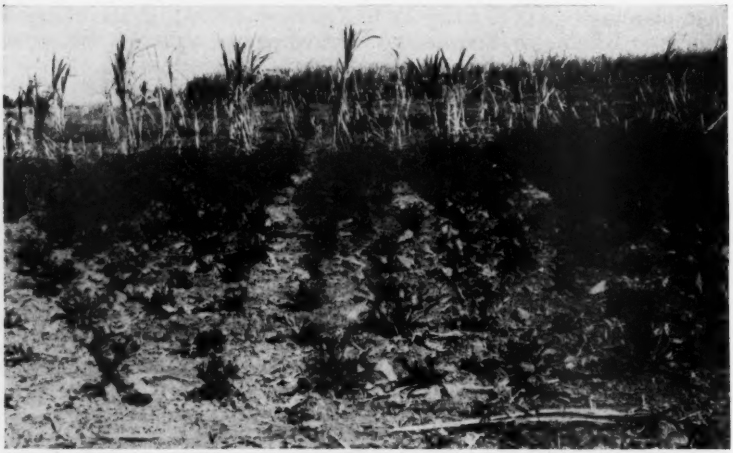

FIGURE 4.—Plot of badly diseased mangel-wurzels adjacent to a plot of tomatoes. Although leafhoppers (*Agalliana ensigera*) were abundant on the mangel-wurzels during most of the season of 1940–41, no curly top was observed on the tomatoes. Photographed at Tucumán, Argentina, December 1940.

appeared excellent. However, none of the tomato plants showed symptoms of curly top at any time.

It is not impossible that strains of curly top virus able to attack tomatoes occur in Argentina despite the fact that none was discovered in the field or through tests with leafhoppers. It seems probable, however, that the disease reported earlier as curly top on tomato is another virus disease that produces symptoms resembling curly top as it is known on tomato in the United States. Fawcett (*12*) has shown recently that the causal virus of this Argentine tomato disease is transmitted by thrips (*Frankliniella paucispinosa* Moult.).

The tomato disease was present in a number of fields in the vicinity of Tucumán and was found in the lower Río Negro Valley. Leaves of affected plants rolled and turned yellow, and in some instances the plants died. In the early stages, however, there were necrotic spots on the young leaves but veinlet clearing was absent. Fawcett (*12*) is of the opinion that this disease is a type of spotted wilt.

Attempts by the senior author to transmit the disease from tomato to sugar beet by means of *Agalliana ensigera* resulted in no infection. Juice inoculation from tomato to *Nicotiana glutinosa* L., *N. tabacum* L. var. Turkish, and × *Petunia hybrida* also resulted in no infection. Fawcett (*13*) was unable to transmit the disease to *Datura stramonium* L. by means of grafts. Spotted wilt virus is reported to cause local lesions on the first three of these species and to cause systemic infection on *D. stramonium*. The general symptoms on tomato, the properties of the virus as determined by Fawcett, and the vector relationship indicate, however, that it may be a strain of the spotted wilt virus, perhaps different from any yet described from other parts of the world. This virus produces a serious disease (corcova) of tobacco in the Province of Tucumán.

If this disease of tomato is caused by a strain of the spotted wilt

virus, it is of interest to note that what is now believed to be the same trouble was described by Fawcett (*11*) in 1930, the year that Samuel, Bald, and Pittman (*19*) reported the virus nature of spotted wilt in Australia. Fawcett's record, therefore, would be evidence of contemporaneous occurrence of spotted wilt in the Western Hemisphere.

Plants Infected Experimentally

Tests were made on a number of species and varieties of plants to determine their susceptibility to the curly top virus found at Tucumán. In order to provide a better basis for comparing the North American and the Argentine curly top, several plants were selected whose reaction to curly top as it occurs in the United States was already known.

The plants tested were grown in pots under cloth cages. Some of the inoculations were made by means of viruliferous *Agalliana ensigera* reared on diseased beets in cages, and others by means of leafhoppers captured on diseased plants in the field. In general, except on seedling beets on which one leafhopper per plant was used, relatively large numbers of insects were placed on each plant, and most of the plants were inoculated several times by means of insects from different sources. The species and varieties of plants inoculated and the results obtained are shown in table 2.

Infection was obtained on all the beet varieties, but the percentages of infection were not so high as those usually obtained with *Eutettix tenellus* and a virulent strain of North American curly top virus.

No infection was obtained on tomato, although large numbers of leafhoppers were used and the plants were inoculated repeatedly by means of leafhoppers from stock colonies as well as leafhoppers from diseased mangel-wurzels and sugar beets in the field. As reported by Fawcett (*11*), young leaves of inoculated plants were rolled, especially on plants on which large numbers of leafhoppers were placed. When the leafhoppers were removed, however, the plants produced normal leaves. The variety of tomato (Manzana) used in these tests was later tested at Riverside, Calif., and found to be susceptible to North American curly top.

Table 2.—*Results of inoculation of different species and varieties of plants with Argentine curly top virus by means of Agalliana ensigera*

Species or variety inoculated	Leafhoppers caged on each plant	Plants inoculated	Plants infected	
	Number	*Number*	*Number*	*Percent*
Beta vulgaris var. S. L. 68	1	78	8	10
Beta vulgaris var. U. S. 11	1	31	13	42
Beta vulgaris var. U. S. 12	1	21	11	52
Beta vulgaris var. R. & G. Old Type	1	40	16	40
Beta vulgaris var. S. L. 842	1	42	10	24
Nicotiana tabacum var. Turkish	25–500	20	0	0
Lycopersicon esculentum var. Manzana	10–500	29	0	0
× *Petunia hybrida*, Rosy Morn type	50–200	10	0	0
Nicotiana glutinosa	25–100	12	0	0
Datura stramonium	2–50	15	0	0
Datura meteloides DC	50	10	0	0
Capsicum frutescens L	15–100	2	0	0
Arachis hypogaea L	25–100	12	0	0
Physalis sp	100	2	0	0
Amaranthus sp	10–100	12	0	0
Stellaria media (L.) Cyr	10	52	27	51
Zinnia elegans Jacq	2–100	10	1	10
Phaseolus vulgaris L	50	11	0	0

Other members of the family Solanaceae also appeared to be resistant or immune. Of the species of this family tested, *Nicotiana tabacum* var. Turkish, *N. glutinosa*, *Datura stramonium*, and $\times$*Petunia hybrida* are susceptible to North American curly top and *D. meteloides* is resistant or immune. Evidence already mentioned, however, indicates that petunia and a species of *Physalis* sometimes become infected under natural conditions in Argentina.

Attempts were made to infect tobacco by means of grafts. In the first of these, sections cut from stems of two petunia plants that showed symptoms identical with those found on petunia in the United States when infected by curly top were inserted into the stems of five Ambalema tobacco plants. Four of the scions soon died, but the fifth lived for more than 5 weeks and produced a small amount of growth. No symptoms were produced on any of the inoculated plants. In a second test, sections of the stem of a plant of *Physalis* sp., known to have curly top virus through tests with leafhoppers, were grafted into the stems of five Turkish tobacco plants. The scions remained alive for more than 3 weeks, but no infection was produced.

Zinnia elegans appears to be very resistant to infection, since only 1 of 10 plants, each inoculated by means of large numbers of leafhoppers, became infected. In other tests leafhoppers placed on large numbers of seedlings in the open produced no infection. Chickweed (*Stellaria media*) appears to be relatively susceptible, although infection was low as compared with that normally obtained with North American curly top virus.

DESCRIPTION OF SYMPTOMS ON VARIOUS HOSTS

Sugar Beet

After the inoculation of cotyledon-stage sugar beets with Argentine curly top by means of *Agalliana ensigera*, symptoms appeared on the young leaves in 4 to 10 days. The first symptoms consisted of veinlet clearing, vein swelling, and leaf rolling. In some cases, rolling and twisting of leaves were very marked even on the varieties U. S. 11 and U. S. 12, resistant to North American curly top. However, severely diseased seedlings were not killed and as they continued to grow the symptoms became progressively less severe. Figure 5, *A*, shows plants of the varieties R. & G. Old Type, U. S. 12, and U. S. 11 inoculated in the seedling stage but partially recovered. U. S. 12 and U. S. 11 show the most marked evidence of recovery; the symptoms on R. & G. Old Type are still rather severe. Figure 5, *B*, shows the plants at a later stage.

Plants inoculated when they had 8 to 10 true leaves also showed severe primary symptoms. The first affected leaves were curled, veinlets were translucent, and the petioles were shorter than on healthy plants. Phloem exudate was abundant on the petioles and main veins of the leaves in many cases. Later growth was more normal in appearance and, with the exception of the varieties R. & G. Old Type and S. L. 842, all recovered to such an extent that they showed only veinlet clearing in the younger leaves and slight vein swelling in the older ones. Even on R. & G. Old Type and S. L. 842, the leaves were almost normal in size and shape, but vein swelling was conspicuous and protuberances and spiny outgrowths from the veins were common. This type of recovery was characteristic of the

FIGURE 5.—*A*, Sugar-beet plants, severely affected with Argentine curly top after inoculation in the cotyledon stage, showing distinct evidence of recovery: *a*, R. & G. Old Type; *b*, U. S. 12; *c*, U. S. 11. *B*, Same plants at a still later stage of development. U. S. 12 (*b*) and U. S. 11 (*c*) have almost completely recovered from the effects of the disease; R. & G. Old Type (*a*) shows only veinlet clearing and vein swelling. Photographed at Tucumán, Argentina, 1941.

regular course of the disease on sugar beet as it was observed on plants in pots and in the field. In contrast, plants affected with North American curly top, at least those of susceptible varieties, show little or no evidence of recovery after infection.

In recently infected beets, phloem necrosis was as characteristic and marked in plants affected with Argentine curly top as it is in those

affected with North American curly top. Necrosis was especially evident in the petioles and larger veins of recently infected plants. Microscopic examinations of transverse sections of petioles revealed blackened phloem areas in which many of the cells had collapsed. Later there was evidence of tissue regeneration similar to that described by Esau (7) in plants affected with North American curly top. Phloem necrosis was marked in roots of all ages in the field and under cages. In the larger beets rings of blackened phloem were evident but rings produced as the plants recovered were less conspicuous. Severity of vascular necrosis appeared to be more or less correlated with severity of leaf symptoms.

Mangel-Wurzel

Diseased mangel-wurzels of the Golden Globe variety, planted and inoculated by G. L. Fawcett, were available for study in October 1940. At that time the plants were small to medium, with roots 1 to 3 inches in diameter, and gave evidence of having been infected when relatively small. There was much variation in severity of symptoms on the different plants. Some were severely stunted, with leaves rolled and crinkled and petioles shortened. Exudate was present on the petioles of many of the younger leaves. When the plants were removed from the soil, it was observed that many of the rootlets had died and others had pushed out, producing a bunchy appearance similar to that found frequently on beets affected with curly top in the United States. In some plants transverse sections of the roots revealed dark rings marking necrosis in the vascular regions. Vascular necrosis appeared to be more marked in the region of the crown than in other parts of the root, but in the specimens examined necrosis was not excessive and in many specimens it was not clearly evident. Necrosis was observed also in the region of the phloem in petioles of the more severely affected leaves.

Some of the plants were mildly affected and appeared normal in size and general appearance. All these plants, however, showed more or less distinct vein swelling on the older leaves and veinlet clearing on the younger ones. Usually, necrosis was not evident in the phloem of roots and petioles of plants of this type. Between these two extremes there were many plants showing various degrees of injury.

Petunia

On two plants of petunia believed to be naturally affected with curly top, the leaves were yellow and curled. Some were distorted and twisted, and the younger ones showed distinct veinlet translucency. Veins of older leaves were conspicuously swollen. Vein swelling and distortion of tissues were evident also on the corolla and calyx. The plants eventually yellowed and died.

Physalis

The young leaves of all the growing points of a large physalis plant found naturally infected were distinctly curled and crinkled. The youngest leaves had clearly defined translucent veinlets. Growth of all shoots was much retarded.

ZINNIA

Primary symptoms on zinnia consisted of veinlet clearing and rolling of the younger leaves, followed by vein swelling. Growth of the terminal of the one plant observed was much reduced, but the plant eventually flowered (fig. 6). The first blossom was small, the color was

FIGURE 6.—Zinnia plant infected with Argentine curly top by exposure to viruliferous *Agalliana ensigera* at Tucumán, Argentina.

partly suppressed, and the petals were reduced in size and distorted and showed distinct vein swellings. Lateral buds grew into shoots that were at first much distorted, with leaves small and curled. The shoots later recovered to a considerable degree and the blossoms were more nearly normal.

CHICKWEED

Only the early stages of the disease on chickweed were observed. Young leaves developed distinct veinlet clearing in periods of from 5 to 8 days after inoculation. As the leaves of affected plants continued to grow they became puckered or curled and twisted. Prominent swollen areas were produced on the veins. The tips of the shoots became distorted and frequently turned downward, and growth was much retarded.

VARIETAL RESISTANCE OF SUGAR BEETS

Limited tests were made to determine the relative resistance of the sugar-beet varieties S. L. 68, U. S. 11, and U. S. 12, known to be resistant to North American curly top, and R. & G. Old Type and S. L.

842, known to be very susceptible to North American curly top. In the tests with potted plants of these varieties, seedlings were inoculated by placing one viruliferous *Agalliana ensigera* on each plant and allowing the insects to feed for 3 days. All inoculated plants were kept in cloth cages until final results were recorded. The results of a series of tests are shown in table 3.

TABLE 3.—*Results of tests to determine relative susceptibility of varieties of sugar beet to Argentine curly top*

Test No.	Plants inoculated [1]		Plants infected	
	Variety	Number	Number	Percent
1	S. L. 68	19	2	11
	R. & G. Old Type	15	4	27
2	U. S. 11	12	7	58
	U. S. 12	12	5	42
3	S. L. 68	38	5	13
	S. L. 842	21	4	19
4	S. L. 68	21	1	5
	U. S. 11	19	6	32
	U. S. 12	19	6	32
	R. & G. Old Type	25	12	48
	S. L. 842	21	6	29

[1] All plants were inoculated in the cotyledon stage by placing 1 viruliferous leafhopper on each plant and allowing it to feed for 3 days.

The same varieties, except S. L. 842, were planted for the field tests October 24 in a plot adjacent to rows of mangel-wurzels infected with curly top and heavily infested by *Agalliana ensigera*. Germination of seed was excellent, and an almost perfect stand of plants was obtained. Leafhoppers began to migrate to this planting as soon as the first seedlings were through the soil, and leafhoppers continued to be present in considerable numbers throughout the time the plot was under observation. Symptoms of curly top began to appear on many of the plants with the production of the first true leaves. The disease continued to spread, and soon after the plants were thinned on November 24 all varieties, except S. L. 68, showed a high percentage of infection. The results of counts of diseased plants made on different dates are shown in table 4.

In the earlier stages of the disease, U. S. 11 showed the highest percentage of infection, probably because it was closest to the badly diseased mangel-wurzels that served as the principal source of infection.

TABLE 4.—*Percentage of curly-top-diseased plants found in varieties of sugar beet in plots at Tucumán, Argentina, on the indicated dates*

[Beets planted October 24, 1940]

Variety	Plants showing symptoms of curly top on—					
	Nov. 12	Nov. 18	Dec. 2	Dec. 10	Jan. 7	Feb. 8
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
U. S. 11	5	22	68	95	100	81
R. & G. Old Type	1	9	56	94	100	100
S. L. 68	Trace	Trace	8	17	82	43
U. S. 12	Trace	1	41	86	100	89

The early symptoms were severe on seedlings of all varieties. Leaves were much distorted, and the younger ones showed marked veinlet translucency. Symptoms were almost as severe on U. S. 11 and U. S. 12 as on R. & G. Old Type, but they were somewhat less severe from the beginning on S. L. 68. Symptoms continued severe until thinning time, November 24. After the plants were thinned, growth was very rapid and by December 16 there was a marked difference in the appearance of the different varieties. Most of the plants of S. L. 68 had recovered to an appreciable degree, the symptoms consisting of slight vein swelling and in some cases a tendency toward crinkling of leaves. U. S. 11 and U. S. 12 also had recovered to a marked degree. The three rows of R. & G. Old Type were beginning to recover, but the foliage was somewhat yellower than that of U. S. 11 and U. S. 12 and more of the lower leaves of the plants of this variety were dying. On December 17 a hot wind blew for several hours, and it was observed that the plants of R. & G. Old Type wilted more than those of the other varieties. However, a photograph taken December 16 (fig. 7) showed little difference in the size of plants of the different varieties.

FIGURE 7.—Plot at Tucumán, Argentina, in which North American varieties of sugar beet were tested for resistance to Argentine curly top. At the extreme right, and only partly in view, are large plants of diseased mangel-wurzels (*a*) that furnished the inoculum for the sugar beets. U. S. 11 (*b*), resistant to North American curly top, occupied three rows to the left of the mangel-wurzels. The next three rows to the left are R. & G. Old Type (*c*), susceptible to North American curly top; farther to the left are the resistant varieties (*d*) U. S. 12 and S. L. 68. In this stage, plants of the different varieties differed little in size. However, symptoms consisting of veinlet clearing, vein swelling, slight leaf rolling, and yellowing of the older leaves were most marked in R. & G. Old Type plants. Under similar conditions of infection with North American curly top, the difference in size between resistant and susceptible plants would be much greater. Photographed December 16, 1940.

By January 7, after 2 weeks of hot, dry weather, approximately 20 percent of the plants of all varieties had died. Plants apparently healthy wilted suddenly and when pulled were found to have rot on the lower portion of the main root. This trouble was apparently distinct from curly top, but the cause was not determined.

At this time, R. & G. Old Type definitely showed more severe symptoms of curly top than the other varieties. The petioles of plants of this variety were slightly but not markedly shortened, the leaves were rolled in some plants, and protuberances and spiny outgrowths were common. There was considerable variation in the severity of the disease on different plants, and this was true also of U. S. 11 and U. S. 12. There was little difference in the average size of plants of the different varieties.

During January these plants were severely attacked by leaf spot caused by *Cercospora beticola* Sacc., and by February 8 many of the older leaves had been killed by this disease. However, the plants had continued to recover from the effects of curly top. Symptoms were indistinct on S. L. 68, and many of the infected plants showed no clearly defined symptoms. This was true also for U. S. 11 and U. S. 12, but to a lesser degree. Certain plants of these latter varieties had clearly defined but rather mild vein swelling, but there was no evidence that the disease had interfered appreciably with growth. Vein swelling and general roughness of leaves were evident on most of the plants of R. & G. Old Type, but there was little evidence of production of leaves with short petioles or of stunting of the plants. Typical diseased plants of R. & G. Old Type and of U. S. 11 are shown in figure 8.

The results of observation of the plants in this plot, together with those made on seedling beets in pots, indicate that of the varieties tested S. L. 68 showed the most resistance, followed by U. S. 11 and U. S. 12. R. & G. Old Type was the most susceptible. This is the order in which these varieties stand in their resistance to curly top in the United States.

THE VECTOR

Characteristics, Distribution, and Host Range

The leafhopper *Agalliana ensigera*, vector of the curly top virus in Argentina, is about the size of *Eutettix tenellus*, vector of North American curly top virus, which it resembles in many of its characteristics and habits. The males are smaller and darker than the females. The nymphs hatch from eggs in about 9 days at a temperature of 100° F. and develop into adults in about 25 days at this temperature. Like *E. tenellus*, this insect has a high temperature optimum for development. The nymphs are somewhat more sluggish than those of *E. tenellus*, and when disturbed usually run to the opposite side of the stem or leaf instead of jumping. Adults usually fly when disturbed. When confined in cages or tubes, they often make a distinctly audible buzzing sound with their wings.

The favorite host plant appears to be the beet. Eggs are laid in beet plants in great numbers, and colonies totaling a thousand or more individuals may be reared on a single large plant. In the Province of Tucumán, the insect was found to be abundant where beets of any

FIGURE 8.—Reaction of two varieties of sugar beet to Argentine curly top. The plants were of the same age and were similarly inoculated. *A*, R. & G. Old Type, showing vein swelling and rugose leaves; *B*, U. S. 11, showing almost no symptoms of curly top. Photographed at Tucumán, Argentina, 1941.

kind were growing. In the vicinity of beet plantings, the insect was found on two species of *Amaranthus*, on one species of *Portulaca*, and on *Datura stramonium*, *Zinnia elegans*, and *Chenopodium album* L. It was not found on any of the native shrubs or on plants outside the cultivated areas.

In the lower Río Negro Valley the leafhopper was very scarce during the month of February 1941, but small numbers were found on sugar beets. In this region plants of Russian-thistle (*Salsola kali* L. var. *tenuifolia* Tausch.), alfileria (*Erodium cicutarium* L'Hér.), *Chenopodium* spp., and mustards were abundant in the plantings of beets and in areas adjacent. Apparently none of these harbored the insect to any appreciable extent. The leafhopper was not captured on any of the native vegetation outside the cultivated area.

The leafhopper breeds readily on mangel-wurzel and red garden beet as well as on sugar beet. It is able to breed also on *Amaranthus* spp., *Datura stramonium*, *D. meteloides*, and *Zinnia elegans*, and to a limited extent on *Chenopodium album*. Of these plants, only mangel-wurzel, beet, and *Amaranthus* spp. appeared to be important in maintaining the leafhopper population observed at Tucumán. Apparently the insect is unable to breed on tobacco and tomato.

The native hosts of *Agalliana ensigera* in Argentina are unknown. The beet is an introduced plant and is grown to only a very limited extent in the Province of Tucumán. It seems probable that it is of little importance in determining the survival of the leafhopper, though it may be of considerable importance in bringing about great local increases in populations of the insect. It seems probable that the natural host plants may not be sufficiently favorable to support a large population of the insect but are able to provide only for its survival at a relatively low population level. Obviously, a more complete knowledge of the host range of *A. ensigera* might open new avenues for study of the reservoirs of the curly top virus in Argentina.

Feeding Habits in Relation to Curly Top Transmission

Although *Agalliana ensigera* may be found in feeding position on all exposed parts of the beet plant, it is commonly found on the smaller leaves and along the two edges of the petioles of the larger leaves. Evidence indicates that it feeds by preference on the vascular bundles.

Microscopic examination of transverse sections of petioles on which large numbers of leafhoppers had fed revealed many clearly evident feeding punctures. These were marked by yellowish deposits of saliva. In many cases the line of puncture extended from the epider. mis directly to a vascular bundle and terminated in the phleom- Deposits of salivary material were evident in the phloem and in tissues outside the phloem.

The punctures extended directly through the cell walls and protoplasmic content, but the punctured cells appeared to suffer no immediate ill effects. The lines of puncture were straight except where they curved to enter the vascular bundles. They were marked by thin and not always continuous sheaths of salivary material introduced by the leafhoppers. Judging from the sections of beet petiole examined, it seems probable that *Agalliana ensigera* introduces less salivary material into the plant than does *Eutettix tenellus* under

similar conditions of feeding. When the leafhopper fed on the petioles of young leaves, drops of clear liquid often appeared above the punctures after the mouth parts were withdrawn. Possibly this may have been due to the introduction of saliva insufficient to plug effectively the puncture made in feeding. If the lines of puncture were plugged incompletely by coagulated saliva introduced by the insect, it might be expected that, since the phloem content is under a positive pressure, liquid content of the phloem would flow out through the holes made by the mouth parts of the insect. This might be true especially if the sheath passing through the parenchyma were more or less complete and if the end entering the phloem were open.

In a study of some of the properties of the virus the ability of the leafhopper to feed on liquids through a membrane was tested before methods of artificial feeding were used. The first tests were made with drops of sugar solution placed on the outer surface of Baudruche capping skin covering one end of a cage in which the insects were confined. A rather thick grade of capping skin was used in these tests. The leafhoppers were able to locate the drops of sugar solution, but it was evident that they had great difficulty in penetrating the capping skin. After finding the drops they extended their legs as if to obtain a firmer footing, placed their proboscises in contact with the membrane, and moved their heads as if attempting to force the mouth parts through the membrane. With the thinner capping skin employed later, it was found that some of the leafhoppers were able to penetrate the membrane. In a few instances, mouth parts could be seen clearly in the drops of sugar solution below the membrane. However, the leafhoppers were restless and the mortality in a 2- to 4-hour period at 100° F. (37.8° C.) was very high.

In further tests, the capping skin was replaced by lens paper lightly impregnated with paraffin. The leafhoppers fed much more readily through this type of membrane than through capping skin. For best results, however, it was necessary to have just enough paraffin to prevent wetting of the paper but not enough to completely fill all the interstices. The leafhoppers did not readily penetrate paraffin films but fed through openings in the paper not closed by the paraffin. With this kind of membrane, the leafhoppers fed reasonably well and, with most of the food materials used, remained alive throughout a feeding period of 4 to 6 hours at a temperature well above 100° F.

When the setae of *Eutettix tenellus* penetrate a membrane and enter a liquid, a salivary secretion flows out of the tips of the setae, immediately gels, and forms a sheath around the mouth parts. Usually, by repeated probing and emission of more salivary secretion, an appreciable deposit of coagulated material is built up. Deposits of this type are visible under low magnification and may be seen also in clear liquids by the unaided eye.

Drops of sugar solution on which individuals of *Agalliana ensigera* were feeding were watched under a hand lens, and penetration of the drops by the mouth parts of many leafhoppers was observed. These observations, however, did not reveal the presence of any coagulable material in the vicinity of the mouth parts. When the setae entered the liquid they came through the membrane free of any indication of introduced material, and throughout the feeding periods the setae remained naked in the liquid. Moreover, no deposits of salivary

material were found in drops on which the leafhoppers had fed for 4 to 6 hours. As already stated, however, deposits of salivary secretions were found in the plant tissues in which the leafhopper fed. This of course shows that *A. ensigera* does produce salivary secretions that are emitted and that coagulate in plant tissue. Failure to observe such deposits in sugar solutions indicates that for some reason the leafhopper introduces little, if any, coagulable salivary secretions when feeding on such liquids.

The evidence indicates that leafhoppers introduce the virus into plants through the medium of the coagulable saliva. This has not been proved definitely, but it is significant that in the case of all leafhopper vectors on which information is available coagulated salivary secretions have been found in the infected plants. Smith (*21*) showed that liquids on which *Eutettix tenellus* fed contained free curly top virus that could be picked up by nonviruliferous leafhoppers. Whether this was introduced into the liquids free of the coagulable saliva or was introduced with it and later diffused out of the coagulum into the surrounding medium was not determined.

Since *Agalliana ensigera* apparently does not introduce coagulable saliva into sugar solutions, experiments were made to determine whether this insect also fails to introduce virus into such solutions. In these tests viruliferous individuals were allowed to feed on drops of sugar solution through a membrane for about 1 hour. The drops were then transferred to a second membrane through which nonviruliferous leafhoppers fed for about 4 hours. The leafhoppers of this second lot were then caged singly on seedling beets. The results of these tests are presented in table 5, together with results of similar tests made at Riverside, Calif., with *Eutettix tenellus* and the North American curly top virus. It may be noted that no infection was obtained from the liquids on which viruliferous *A. ensigera* had fed, whereas relatively high percentages of infection were obtained from liquids on which viruliferous *E. tenellus* had fed.

TABLE 5.—*Results of tests to determine whether viruses of North American curly top and Argentine curly top are introduced into sugar solutions during the feeding of viruliferous individuals of Eutettix tenellus and Agalliana ensigera, respectively*

Species of leafhopper tested	Test No.	Plants inoculated [1]	Plants infected	
		Number	*Number*	*Percent*
Agalliana ensigera [2]	1	12	0	0
	2	14	0	0
	3	6	0	0
Eutettix tenellus [3]	1	20	11	55
	2	19	9	47
	3	20	14	70

[1] Nonviruliferous leafhoppers of each species, fed on sugar solutions on which viruliferous leafhoppers of the same species had previously fed, were allowed to feed on the test sugar-beet plants.
[2] Tested at Tucumán, Argentina, November 1940.
[3] Tested at Riverside, Calif., April 1939.

Although the tests with *Agalliana ensigera* are somewhat limited, the apparent absence of virus from the liquids in which no coagulated salivary deposits were observed is further indication that the introduction of virus into a medium by a leafhopper is associated with the introduction of coagulable salivary secretions. If virus is introduced into plants directly with the coagulable saliva the quantity of virus

would tend to be proportional to the amount of saliva introduced in insect feeding. Since it seems probable, on the basis of observations so far made, that *A. ensigera* introduces less coagulable saliva into the plant than does *Eutettix tenellus*, this may be a factor influencing adversely the efficiency of *A. ensigera* as a vector.

THE VIRUS

Incubation Period in Vector

The period that must elapse between the time *Eutettix tenellus* begins to feed on a diseased plant and the time it is able to transmit the virus of North American curly top to a healthy plant has been found to be as short as 4 hours in some instances. Assuming that the incubation period of the Argentine curly top virus in *Agalliana ensigera* also would be short, preliminary experiments were made in which nonviruliferous leafhoppers were allowed to feed on a diseased plant for 2 hours and were then transferred at hourly intervals to sugar-beet seedlings. When these tests gave no infection, the time the leafhoppers were allowed to feed on the diseased plants and on the seedlings was increased. The results of six tests are shown in table 6.

The infection obtained was less than would be expected with North American curly top virus and *Eutettix tenellus*, but the number of plants inoculated probably was not large enough to provide an accurate estimate of the minimum incubation period of the Argentine curly top virus in its vector. However, the fact that infection was usually produced by insects that had fed from 24 to 72 hours shows that the incubation period of the virus in the insect is relatively short. More extensive tests are needed to determine whether in certain individual insects it may be considerably shorter than that indicated by the results obtained in this series of tests.

Period of Retention in Vector

On November 12, 1940, about 200 large nymphs and young adults of *Agalliana ensigera* were removed from a plant of sugar beet affected with Argentine curly top, placed on a vigorous plant of *Chenopodium album*, and allowed to remain there until December 18. By that time mortality was high, but 11 adults of the leafhoppers originally introduced were recovered and caged singly on seedling sugar beets. By January 3, 5 of the 11 plants had become diseased, clearly indicating that the leafhoppers still carried the virus. When the adult leafhoppers were removed from the *C. album* plant, it was found that a number of half-grown and smaller nymphs were present that had developed from eggs laid by the original viruliferous leafhoppers. Of these, 32 were caged on 16 seedling sugar-beet plants. None of these plants developed symptoms of curly top. Since nymphs developed from eggs deposited on *C. album* were unable to obtain virus by feeding on its juices, it appears that this plant is immune to curly top. This being true, the viruliferous adult leafhoppers placed on the plant November 12 did not increase their virus content through feeding and, since they still contained virus on December 18, it is evident that *A. ensigera* is able to retain the virus of Argentine curly top in its body for at least 36 days. It is also evident that the virus does not pass through the egg stage of the insect.

TABLE 6.—*Incubation period of Argentine curly top virus in Agalliana ensigera*

Test No.	Period of leafhopper feeding on diseased beets	Number of sugar-beet plants inoculated and infected by leafhoppers in which the virus had the indicated incubation period (hours)																											
		3		4		5		6		7		8		24		48		72		96		120		144		192		240	
		Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected
	Hours																												
1	2	3	0	4	0	3	0	4	0	2	0	3	0	1	0														
2	3							4	0					5	1	5	0			3	2			5	2			3	0
3	3							4	0					4	0	4	1			4	2	2	0	2	1			3	1
4	24															4	1	3	0							3	0		
5	24															4	0	4	1							4	2		
6	4									19	0			16	0	16	1	17	0										

Occurrence in Phloem Exudate

In view of the fact that exudate from the phloem of diseased beets has proved to be the most satisfactory medium from which to recover the virus of North American curly top, tests were made to determine whether the curly top virus in Argentina could also be recovered from phloem exudate. Small quantities of exudate produced naturally on the petioles of diseased plants were collected by means of a capillary tube. The exudate was diluted about 1 part to 9 parts of distilled water and fed to nonviruliferous leafhoppers. After a feeding period of about 6 hours, the leafhoppers were caged singly on seedling beets. Of 12 plants inoculated, 4 became infected.

Properties

Phloem exudate [8] diluted 1 part of exudate to 9 parts of distilled water was used in a series of tests to determine the thermal inactivation point of the virus. The diluted exudate was placed in small test tubes (about 2 cc. per tube). The tubes were then covered with rubber caps and placed in a water bath held as nearly as possible at the desired temperature for 10 minutes. After treatment the tubes were removed from the bath and placed immediately in cold water. Nonviruliferous leafhoppers were allowed to feed on the treated exudate for about 6 hours and were then caged singly on seedling sugar beets. The results of three tests are shown in table 7, together with the results of one test in which alcoholic precipitate from viruliferous leafhoppers was used as the source of virus.

Infection was relatively low in all tests. For this reason the results are not so conclusive as they would be had higher percentages of infection been obtained. The results indicate, however, that the thermal inactivation point of the virus lies between 75° and 80° C. This is also the range in which the curly top virus of North America is inactivated.

Table 7.—*Results of tests to determine the thermal inactivation point of virus of Argentine curly top*

Test No.	Number of sugar-beet plants inoculated and infected by means of leafhoppers that fed on virus suspensions heated for 10 minutes at the indicated temperature (°C.)													
	Check, not treated		55		60		65		70		75		80	
	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected	Inoculated	Infected
1	10	1			10	0			10	0				
2	12	6	11	6	8	1	10	4						
3 [1]	3	0					7	1	5	0	8	2	5	0
4	16	2					16	1	19	1	20	1	17	0

[1] The source of virus in this test was a wash of alcoholic precipitate of macerated, viruliferous leafhoppers.

[8] Tests were made with the exudate from the cut surface of large diseased roots of mangel-wurzel. To obtain exudate, the roots were taken from the field and placed in pails of water in the laboratory. Cuts were made across the crowns of the roots to induce flow of liquid from the phloem. In most cases the roots did not exude appreciably the first day but on the second, third, and fourth days flow was more abundant. In some cases it was possible to collect as much as a cubic centimeter of exudate from lots of six or more roots. This exudate was used for further studies of the virus.

Dilution tests were made in which phloem exudate was diluted with distilled water, 1 part of exudate in 10 parts of the mixture; 1 part of exudate in 100 parts; and 1 part of exudate in 1,000 parts. Nonviruliferous leafhoppers were allowed to feed on these mixtures for about 6 hours and then were caged singly on seedling sugar beets. From each dilution 12 plants were inoculated. Only 1 plant became infected, and this was by a leafhopper that had fed on the 1-in-10 dilution.

Attempts were made to recover virus from different types of precipitates. Juice from diseased beets was precipitated in 50-percent alcohol. The precipitate was recovered by filtration, dried at laboratory temperature, and mixed with 5-percent sugar solution. The filtrate from this was fed to nonviruliferous leafhoppers that were later caged singly on seedling sugar beets. Tests were made with fresh beet juice and with juice held at laboratory temperatures for 1, 2, and 3 days. No infection was produced by leafhoppers that fed on these mixtures.

In tests involving also thermal inactivation, essentially the same technique as that described above for virus recovery was used but the source of virus was macerated, viruliferous leafhoppers. Infection was obtained from a wash of the alcoholic precipitate of macerated leafhoppers. These results are given in test 3 of table 7. The heat treatments superimposed on the wash are not interpreted as having significant influence on the release of virus.

Phloem exudate, dried and kept at laboratory temperatures, was tested for virus content at intervals of 2 weeks over a period of 2 months. The exudate in these tests gave little infection when fresh, and no virus was recovered from the dried material.

Transmission by Mechanical Inoculation

Sugar-beet plants of the variety U. S. 11, having about six true leaves and growing rapidly, were inoculated by needle with phloem exudate as a source of virus. The exudate was obtained as clear drops from the surface of petioles of recently infected sugar-beet plants and was placed in the axils of the leaves at the crowns of the healthy beet plants. Numerous punctures were made with a very fine needle through these drops of exudate into the crowns of the plants. Of 20 plants inoculated in this manner 4 became infected. Twenty noninoculated plants held as controls remained healthy.

In a second type of test, phloem exudate was collected from diseased mangel-wurzels, diluted about 1 part of exudate to 4 parts of distilled water and rubbed over the surface of leaves of rapidly growing sugar beets of the variety U. S. 11. Leaves were inoculated with and without the use of an abrasive. Thirty-seven plants were inoculated, but no infection resulted.

More extensive tests are needed to determine whether a relatively high percentage of infection could be obtained consistently by needle inoculation. The same technique has given infection with the virus of North American curly top, but the percentage of infection, with few exceptions, was very low. No infection with North American curly top virus has been obtained in extensive tests in which inoculum was rubbed over the surface of leaves.

Rate of Movement in Beet Leaves

Twenty-four numbered pots, each containing two rapidly growing beet plants having about eight true leaves each, were used in a test to determine the rate of movement of the curly top virus out of inoculated leaves. These plants had grown in semishade and each plant had at least one leaf longer than 15 cm. Ten viruliferous leafhoppers were caged on the tip of one of the longer leaves of each plant at a temperature somewhat above 100° F. (37.8° C.) for 2 hours. At the end of the 2-hour feeding period, the inoculated leaves of all the plants in pots with even numbers were severed at a distance of 15 cm. from the part on which the leafhoppers fed. At the same time the leafhoppers were removed from the leaves of the plants in pots with odd numbers. This second group of plants was retained as a check on the amount of infection produced by the feeding of the leafhoppers.

Three of twenty-four plants from which the leaves were removed and 4 of 24 plants from which the leaves were not removed became infected. This result indicates that the virus is able to move downward from the point of inoculation at a very rapid rate, the measured movement being at least 15 cm. in 2 hours.

DISCUSSION

Relationship of Argentine and North American Viruses

The considerations of major interest and importance in relation to the Argentine curly top disease are (1) its relationship to North American curly top and (2) its potential capacity for injury if introduced into the sugar-beet areas of the United States and other parts of the world.

Certain differences in characteristics of curly top in the two continents are evident, but these differences are not extensive. The vector of the North American curly top virus did not transmit the Argentine virus. The Argentine virus so far as is known does not infect tomato and tobacco. However, Giddings (*14*) has shown that certain strains of the North American virus also do not infect tomato and tobacco. In general, the disease caused by the Argentine virus is characterized by more severe curling and distortion on seedlings of varieties resistant to North American curly top, but infected plants of both resistant and susceptible varieties recover to a marked degree. No comparable recovery has been noted in beet plants infected by the North American virus, especially in those of susceptible varieties.

The similarities between the two diseases are very striking. The symptoms are almost identical on all host plants on which the two diseases have been observed. All varieties of sugar beet developed for resistance to the North American virus that were tested were found to be resistant to the Argentine virus. In general, except for certain members of the Solanaceae, the host range of the two viruses, so far as known, is the same. Properties of the two viruses, insofar as they have been determined, are the same or very similar.

The occurrence of two similar diseases in regions so widely separated as the United States and Argentina, in the absence of any evidence of a common origin, leaves the question of their relationship

rather difficult to determine. At one time, the fact that the vector of the North American virus does not transmit the South American virus would have been accepted as strong evidence that the viruses of the two continents are distinct and separate in spite of the close similarity of symptoms and host range. However, Black's finding (*2*, *3*) that there are two strains of the potato yellow dwarf virus each transmitted by a different leafhopper weakens the confidence that can be placed in differences with respect to the insect vector in the determination of relationships of viruses.

It may be suggested that superimposition of the North American virus on the Argentine virus indicates that the two viruses are unrelated, since it has been maintained that with certain mosaic viruses complete invasion of a plant by one virus confers immunity from infection by a related virus but not by an unrelated virus. However, Carsner (*5*), using sugar-beet plants infected by an attenuated strain of the curly top virus, was able to reinfect them by a more virulent strain, with the result that the plants became more severely diseased. Giddings (*15*), working with 7 clearly differentiated strains of the North American virus, found that beet plants infected for at least a month by one strain of the virus were susceptible to infection by a second strain in 15 combinations tested. Less virulent strains infected plants previously infected by more virulent strains, and more virulent strains were readily introduced into plants already infected by those less virulent. Therefore, the fact that plants infected by Argentine virus remained susceptible to infection by North American virus cannot be accepted as evidence of unrelatedness unless the highly improbable assumption is made that all the strains of North American virus tested are not strains of one virus but are so many separate and distinct viruses.

Because of the marked similarities between curly top of Argentina and that of North America and the wide differences between the characteristics of curly top and all other virus diseases, it seems logical to assume, for the present at least, that curly top of sugar beets in the Western Hemisphere is caused by a single virus complex consisting of different strains and varieties and to classify the Argentine virus as a variety of this curly top virus complex.

In the Latin system of virus nomenclature suggested by Holmes (*17*), the curly top virus is given the name *Chlorogenus eutetticola* H. Carsner and Bennett (*6*), however, suggested that the species be shifted to the genus *Ruga* of Holmes on the basis of symptoms induced and that the species name be changed to *verrucosans*. The variety name *distans*, meaning distant, is suggested as a distinguishing epithet for the Argentine virus. The following description of this virus is presented.

PROPOSED NAME AND DESCRIPTION OF ARGENTINE VIRUS

Ruga verrucosans C. and B. var. **distans** n. var.

Virus causing a disease of sugar beet (*Beta vulgaris* L.), red garden beet, chard, mangel-wurzel, chickweed (*Stellaria media* (L.) Cyr.), and zinnia (*Zinnia elegans* Jacq.). Probably most species of Solanaceae, including tobacco (*Nicotiana tabacum* L.) and tomato (*Lycopersicon esculentum* Mill.), very resistant or immune, but typically diseased specimens of *Petunia* sp. and *Physalis* sp. have been found. Disease on *Beta* spp. characterized by leaf curling, veinlet clearing,

vein swelling, vein roughening, and necrosis of phloem. Recovery of sugar beets more marked with Argentine than with North American virus. Transmitted in nature by *Agalliana ensigera* Oman but not by *Eutettix tenellus* (Bak.). Under certain conditions transmissible to small percentage of plants inoculated by needle; not transmissible by rubbing technique. Remains active in insect vector at least 36 days; does not pass through egg stage of vector. Not inactivated by short exposure to 50-percent alcohol. Thermal inactivation point probably between 75° and 80° C.

Type locality.—Province of Tucumán, Argentina.

SIGNIFICANCE OF VIRUS TO OTHER SUGAR-BEET-GROWING COUNTRIES

Although, so far as known, the Argentine curly top virus is limited in its distribution to the northern half of Argentina, the chances of spread of the virus to other countries, through introduction of the vector or of diseased material or of both, have greatly increased in recent years as a result of the development and extensive use of facilities for more rapid transportation.

The economic consequences of the introduction of the Argentine curly top virus into other sugar-beet-producing countries cannot be predicted accurately because of the impossibility of judging, among other things, its effect on all of the possible host plants under a variety of climatic conditions. However, evidence seems ample to justify the assumption that on sugar beet a high degree of control of the disease could be obtained in all sugar-beet-producing areas by using varieties of sugar beet that have been developed in the United States for resistance to the North American curly top.

SUMMARY

Studies of the Argentine curly top disease of sugar beet were made at Arlington, Va., in 1927 and 1937–39, on diseased material from Argentina. Further studies of the disease were made at the Estación Experimental Agrícola de Tucumán in Argentina in the period from September 1940 to March 1941.

Symptoms on Argentine plants grown in the quarantine greenhouse at Arlington, Va., were similar to those on plants affected with North American curly top. However, *Eutettix tenellus*, the vector of the North American curly top virus, failed to transmit the Argentine virus.

In the Province of Tucumán, Argentina, curly top was found on sugar beet, red garden beet, mangel-wurzel, chard, *Physalis* sp., and probably on × *Petunia hybrida*. It was transmitted experimentally to chickweed, zinnia, and several varieties of sugar beet, but not to any member of the family Solanaceae, including tomato, Turkish tobacco, *Nicotiana glutinosa*, Ambalema tobacco, red pepper, and petunia.

Symptoms of the disease on sugar beet, red garden beet, mangel-wurzel, chard, chickweed, and zinnia, consisting of veinlet clearing, vein swelling, vein protuberances, leaf rolling, and phloem necrosis, were similar to those produced by North American curly top on these plants. In general, symptoms of Argentine curly top were more severe on seedling sugar beet than those of North American curly top, especially in the case of varieties resistant to the North American virus. However, seedlings affected with the Argentine curly top

recovered to a marked degree from the initially severe effects of the disease. Plants that had passed through the recovery phase showed mild to almost no symptoms of disease, depending on the resistance of the variety. Sugar-beet plants affected with North American curly top have not been observed to recover to any appreciable extent.

In tests involving potted plants in cloth cages and in field plots, the varieties S. L. 68, U. S. 11, and U. S. 12, known to be resistant to North American curly top, were found resistant also to Argentine curly top. The variety R. & G. Old Type, very susceptible to North American curly top, was found relatively susceptible to Argentine curly top.

On the grounds of the Estación Experimental Agrícola de Tucumán, the vector of Argentine curly top, *Agalliana ensigera*, was abundant through the season 1940–41 on mangel-wurzels and sugar beets and was found in smaller numbers on *Amaranthus* spp., *Portulaca* sp., *Datura stramonium*, *Zinnia elegans*, and *Chenopodium album*. It was apparently very rare, however, on plants outside the cultivated area. It multiplied readily on sugar beet and mangel-wurzel and was able to breed on *Amaranthus* spp., *D. stramonium*, *D. meteloides*, *Z. elegans*, and to a limited extent on *C. album*. It failed to breed on tomato, Turkish tobacco, and *Nicotiana glutinosa*.

Agalliana ensigera feeds on the phloem of sugar beet and leaves a partial sheath of salivary secretion along the line of puncture. It is able to pick up virus from liquids containing phloem exudate of diseased beets but, unlike *Eutettix tenellus*, the vector of North American curly top virus, it was not observed to leave salivary deposits in the liquid media on which it fed. The minimum incubation period of the virus in the insect, as found, was 24 to 72 hours. Virus in viruliferous insects was not exhausted by a 36-day feeding period on a plant immune to curly top. Limited tests indicate that the virus does not pass through the egg stage of the insect.

The virus of Argentine curly top appears to occur in relatively high concentration in the phloem of infected sugar beets and mangel-wurzels. The thermal inactivation point seems to be between 75° and 80° C. The virus was not inactivated by a short exposure to 50-percent alcohol. By means of phloem exudate from infected sugar beets, the virus was transmitted to 4 of 20 rapidly growing sugar beets by needle inoculation, but no infection resulted from rubbing inoculum over the surface of leaves. The virus moved from the point of introduction by leafhopper inoculation at the distal end of a beet leaf downward through the leaf, a distance of 15 cm., in 2 hours. These properties of Argentine curly top virus parallel those of North American curly top virus, so far as known.

The Argentine curly top virus differs from curly top virus in North America in vector relations and degree of recovery of affected plants as the disease progresses. It resembles curly top virus of North America in the general type of symptoms on known host plants, in host range, so far as is known, except for members of the family Solanaceae, in known properties, and in the resistance manifested by tested sugar-beet varieties. These similarities appear so significant that, despite the differences in vector relations and certain known symptomological and host differences, it seems best to classify, tentatively at least, the

Argentine curly top virus as a variety of the curly top virus complex (*Ruga verrucosans* C. and B.) of North America. The variety name *distans* is suggested for the Argentine virus.

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